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New World geometrid moths (Lepidoptera: Geometridae): Molecular phylogeny, biogeography, taxonomic updates and description of 11 new tribes

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Abstract. We analysed a molecular dataset of 1206 Geometroidea terminal taxa. In this paper we focus on New World taxa, with 102 Nearctic terminal taxa (97 of which have not previously been subject to molecular phylogenetic analysis) and 398 Neotropical terminal taxa (375 not previously analysed). Up to eleven molecular markers per specimen were included: one mitochondrial (COI) and ten protein-coding nuclear gene regions (Wingless, ArgK, MDH, RpS5, GAPDH, IDH, Ca-ATPase, Nex9, EF-1alpha, CAD). The data were analysed using maximum likelihood approach as implemented in IQ-TREE and RAxML. Photographs of almost all voucher specimens are provided together with relevant type material in illustrated electronic catalogues in order to make identities and taxonomic changes transparent. Our analysis concentrates on the level of tribes and genera, many of which are shown to be para- or polyphyletic. In an effort towards a natural system of monophyletic taxa, we propose taxonomic changes: We establish 11 new tribe names (Larentiinae, authors Brehm, Murillo-Ramos & Õunap): Brabirodini **new tribe**, Chrismopterygini **new tribe**, Psaliodini **new tribe**, Pterocyphini **new tribe**, Rhinurini **new tribe**, Ennadini **new tribe**, Cophocerotini **new tribe**, Erebochlorini **new tribe**; (Ennominae, authors Brehm, Murillo-Ramos & Sihvonen): Euangeronini **new tribe**, Oenoptilini **new tribe**, Pyriniini **new tribe**. We assign 27 genera for the first time to a tribe, propose 29 new tribe assignments and 26 new generic combinations, we synonymize one tribe and seven genera, revive one tribe, and propose to exclude 119 species from non-monophyletic genera (*incertae sedis*). Our study provides the data and foundation for numerous future taxonomic revisions of New World geometrid moths. We also examine broad-scale biogeographic patterns of New World Geometridae: While Nearctic species are often nested within the predominantly Neotropical clades, the austral South American fauna forms distinct clades, hinting at a long isolation from the remaining New World fauna.

Key words. Geometridae, new tribes, molecular phylogeny, paraphyly, polyphyly, systematics.

1. Introduction

In the family Geometridae, approximately 24,000 valid species are known (Nieukerken et al. 2011; AH, unpublished data), but many others are still undescribed. Increasing evidence shows that many genera are much more diverse than previously thought, particularly tropical lineages with small and inconspicuous species, e.g., *Drepanogynis* Guenée, [1858] (Krüger 2002), *Eois* Hübner, 1818 (Brehm et al. 2011), *Prasinocyma* Warren, 1897 (Hausmann et al. 2016) and *Oospila* Warren, 1897 (Lindt et al. 2018). Geometridae show a worldwide distribution, but the Neotropical region is more species-rich than any other, with the wet tropical Andes being the global diversity hotspot of the family (Brehm et al. 2016). The group is well defined by apomorphies such as a tympanal organ (with an "ansa") situated at the base of the abdomen in the adult moth, and the reduction of larval prolegs (e.g. Minet & Scoble 1999). The monophyly of the family is well supported in molecular phylogenies (e.g. Heikkilä et al. 2015; Murillo-Ramos et al. 2019). The relationships between the large subfamilies have become rather clear based on molecular phylogenetic studies over the last two decades (Abraham et al. 2001; Yamamoto & Sota 2007; Wahlberg et al. 2010; Strutzenberger et al. 2017; Sihvonen et al. 2011; Õunap et al. 2016), but the position and definition of the enigmatic subfamilies Oenochrominae and Desmobathrinae have been a puzzle until very recently (Murillo-Ramos et al. 2019).

This study is part of a series of papers on the phylogeny of Geometridae. Our common dataset comprises 1206 terminal taxa of Geometroidea from all biogeographic regions (except Antarctica), with a focus on the species-rich Neotropical and the Nearctic fauna. Since these biogeographically important regions have been neglected in previous studies, we expected them to hold the greatest potential with regard to remaining knowledge gaps in phylogeny and systematics. Our paper deals in principle with all New World taxa of the large dataset, and indeed by far most taxonomic changes concern New World taxa, with a focus on Larentiinae and Ennominae. Other papers deal with the relationships of the major lineages of Geometridae at the global level, including the Oenochrominae, Desmobathrinae and the description of the new subfamily Epidesmiinae (Murillo-Ramos et al. 2019); Sterrhinae (Sihvonen et al. accepted); Larentiinae (E. Õunap et al. in prep.), Boarmiini (L. Murillo-Ramos et al. in prep.), and diversification patterns across the family (H. Ghanavi et al. in prep.).

There has been substantial progress in the systematics of Geometridae during recent decades, including landmark book series such as the "Moths of Borneo" (Holloway 1994, 1996, 1997) and "Geometrid moths of Europe" (Hausmann 2001, 2004; Mironov 2003; Hausmann & Viidalepp 2012; Skou & Sihvonen 2015; Müller et al. 2019). No comparable works at such a broad scale have been published for the Neotropical region, with the notable exception of papers on genera of Neotropical Geometrinae (Pitkin 1996) and Ennominae (Pitkin 2002). Further recent systematic works focused on certain genera or tribes and / or regions (examples, list not comprehensive): in Sterrhinae on the Cyllopodini (Lewis & Covell 2008); in Larentiinae on Chilean *Eupithecia* Curtis, 1825 (Rindge 1987, 1991), on Chilean Trichopterygini (Parra 1991, 1996; Parra & Santos-Salas 1992a,b; Parra et al. 2009a, 2017), on *Hagnagora* Druce, 1885 (Brehm 2015), and *Callipia* Guenée, [1858] (Brehm 2018); in Ennominae on Chilean Diptychini (= Lithinini, see Discussion) (Rindge 1986; Parra 1999a,b; Parra & Hernandez 2010; Parra et al. 2009b, 2010), on Chilean and Argentinian Nacophorini (Rindge 1971, 1973, 1983), on Palyadini (Scoble 1994), on *Pero* Herrich-Schäffer, [1855] (Poole 1987), on *Syncirsodes* Butler, 1882 (Bocaz & Parra 2005), on *Thysanopyga* Herrich-Schäffer, [1855] and *Perissopteryx* Warren, 1897 (Krüger & Scoble 1992), and on *Ischnopteris* Hübner, [1823], *Stegotheca* Warren, 1900 and *Rucana* Rindge, 1983 (Pitkin 2005). In Geometrinae, Viidalepp (2017) investigated the phylogeny of Nemoriini; further studied genera include *Chavarriella* Pitkin, 1993, *Dioscore* Warren, 1907, *Lissochlora* Warren, 1900 and *Nemoria* Hübner, 1818 (Lindt et al. 2014a; Pitkin 1993), *Haruchlora* Viidalepp & Lindt (Viidalepp & Lindt 2014a), *Oospila* Warren, 1897 (Viidalepp 2002; Viidalepp & Lindt 2016; Lindt et al. 2018), *Paromphacodes* Warren, 1897 (Lindt et al. 2017), *Pyrochlora* Warren, 1895 (Viidalepp 2009), *Tachyphyle* Butler, 1881 (Viidalepp & Lindt 2017) and *Telotheta* Warren, 1895 (Lindt & Viidalepp 2014b). Broad-scale authoritative works on the Nearctic fauna are limited to the Geometrinae (Ferguson 1985) and Macariini (Ferguson 2008). The Nearctic fauna was treated in part (Canada) by McGuffin (1967, 1972, 1977, 1981, 1987, 1988) and Bolte (1990).

Some New World taxa have been included in previous molecular phylogenetic works, in particular in those focusing on *Eois* (Strutzenberger et al. 2010, 2017) and the subfamily Larentiinae (Õunap et al. 2016). However, New World taxa were heavily underrepresented in other phylogenetic works, for example in studies with a focus on the Asian taxa of Geometrinae (Ban et al. 2018) and Boarmiini (Jiang et al. 2017). In a global phylogeny of Geometridae (Sihvonen et al. 2011), New World taxa were represented with rather few specimens (only 36 out of 149 samples). For our study, we targeted New World taxa in order to address this deficiency: Of a total 1206 terminal taxa, our study comprises 102 Nearctic terminal taxa (97 taxa not previously analysed) and 398 Neotropical terminal taxa (375 taxa not previously analysed).

The primary objective of this paper is to uncover the phylogenetic relationships of a large number of New World Geometridae genera in a global context, and to identify paraphyletic genera and tribes. Many New World geometrid tribes and genera are currently non-monophyletic, and many genera are not even assigned to tribes, despite Pitkin's (1996, 2002) studies. In species-rich genera, our sampling often includes two or more species. Material of the type species of genera or closely

related species was preferably included. Striking examples of polyphyly include *Larentia* Treitschke, 1825 (at four different positions in the tree, see Results) and *Perizoma* Hübner, [1825] (at six positions, see also Õunap et al. in press).

Moreover, we also aim to formally establish taxonomic changes that are required for a system of monophyla, i.e. we attempt to translate as many results as possible into an updated taxonomy of Geometridae. This appears to still be the exception rather than the rule in phylogenetic research, but see e.g. Zahiri et al. (2011) Õunap et al. (2016), Murillo-Ramos et al. (2019), Dhungel & Wahlberg (2018) as examples. Such taxonomic changes will be useful for all biologists working with these organisms who require phylogenetic information and a corresponding modern taxonomy including named entities of their study organisms. Taxonomic changes of our paper focus on the two most species-rich subfamilies Ennominae and Larentiinae, while more such changes are performed in the other papers of the series (see above).

Beyond phylogenetic systematics and taxonomic changes, we also investigate broad-scale biogeographic patterns of New World Geometridae in the context of global phylogeny. We aim to draw preliminary conclusions about the biogeographic origin of certain clades, i.e. whether New World lineages are nested within Old World taxa and vice versa. We also aim to investigate the relationship between Nearctic taxa and Neotropical taxa. It is well known that the austral South American flora and fauna differs considerably from the central and northern parts (Morrone 2015). Holt et al. (2013), analysing distribution and phylogenetic relationships of vertebrates, placed the vertebrate fauna of all of South America into the Neotropical faunal realm. We therefore analyse the austral South American geometrid fauna separately from the fauna of the remaining continent.

2. Material and Methods

2.1. Sampling and documentation

A total of 93 tribe-level taxa (worldwide) are included in this study following current phylogenetic hypotheses and classifications (Pitktin 1996, 2002; Sihvonen et al. 2011, 2015; Wahlberg et al. 2010; Õunap et al. 2016). In addition, 14 non-Geometridae species belonging to the superfamily Geometroidea (Sematuridae, Epicopeiidae, Pseudobistonidae and Uraniidae) were included as outgroups based on the hypothesis proposed by Regier et al. (2009). Where possible, two or more samples were included per tribe and genus, especially for species-rich groups that are widely distributed and in cases where genera were suspected to be poly- or paraphyletic (see Murillo-Ramos et al. 2019 for further details). Identities of species were investigated by the authors and consulted experts and in most cases confirmed by comparing the COI region ('DNA barcode') with sequence data available on BOLD systems (Ratnasingham & Hebert 2007).

Photographs of adult moths were taken of the examined material as well as of relevant type material and compiled in three large illustrated pdf catalogues (supplementary material, see Methods). These catalogues provide an excellent overview of taxa (e.g. Kawahara et al. 2018), and they allow readers to easily check the validity of results and critically assess our taxonomic changes.

2.2. Molecular techniques

DNA was extracted from 1–3 legs preserved either in ethanol or dry. In a few cases, other sources of tissue, such as parts of larvae, or full abdomens of adults, were used. The remaining parts of specimens were preserved as vouchers and deposited in public museum collections. Genomic DNA was extracted and purified using Nucleo Spin® Tissue Kit (MACHERY-NAGEL), according to the manufacturer's protocol. DNA amplification and sequencing were carried out following protocols proposed by Wahlberg & Wheat (2008) and Wahlberg et al. (2016). PCR products were visualized on agarose gels. PCR products were cleaned enzymatically and sent to Macrogen Europe (Amsterdam) for Sanger sequencing. One mitochondrial (COI) and 10 protein-coding nuclear gene regions (Wingless, ArgK, MDH, RpS5, GAPDH, IDH, Ca-ATPase, Nex9, EF-1alpha, CAD) were sequenced.

2.3. Alignment and cleaning sequences

Multiple sequence alignments were done for each gene based on a reference sequence of Geometridae downloaded from the database VoSeq (Peña & Malm 2012). We used MAFFT algorithm as implemented in Geneious v.11.0.2 (Biomatters, www.geneious.com). Sequences with bad quality and ambiguities were removed from the alignments. Finally, aligned sequences were uploaded to VoSeq (Peña & Malm 2012) and then assembled in a dataset comprising 1206 taxa. The final dataset had a concatenated length of 7665 bp with gaps. To check for potential misidentifications, DNA barcode sequences were compared to those in BOLD (Barcode of Life Data Systems) (Ratnasingham & Hebert 2007). After cleaning, the final dataset included at least three genes per taxon except nine samples (see Murillo-Ramos et al. 2019).

2.4. Tree search strategies and model selection

We ran maximum likelihood analyses with a dataset partitioned by codon position. Different substitution models were determined implementing ModelFinder (Kalyaan-

amoorthy et al. 2017). Dataset with different partitions and models were analysed using IQ-TREE (Nguyen et al. 2015) with the MFP+MERGE option (see Murillo-Ramos et al. 2019). Support for nodes were evaluated with 1000 ultrafast bootstrap (UFBoot2) approximations (Hoang et al. 2017) and SH-like approximate likelihood ratio test (Guindon et al. 2010) as implemented in IQ-TREE. Trees were visualized and edited in FigTree v1.4.3 software (Rambaut 2012). The final tree was rooted with non-Geometridae species (see Murillo-Ramos et al. 2019 for further details).

2.5. Taxonomic changes

We propose taxonomic changes if our taxon sampling appears sufficient (including species-richness, and/or morphological diversity and/or geographical extend of the lineage) and we are confident with the results, i.e. our conclusions are supported by high branch-support values (SH > 80 or UFBoot2 > 95) in the molecular phylogeny. Further requirements are that our classification identifies monophyletic lineages, we have adequate morphological material available to us, and identity of examined material is confirmed and can be tracked. It is thus of crucial importance that material of type species of genera or morphologically very similar material was used. Our conclusions are primarily based on molecular results. It is beyond the scope of our paper to perform supplementary morphological analyses, but where available, we have used published information on the morphology, in particular in Ennominae (Pitkin 2002). We nevertheless take obvious morphological features into account for taxonomic decisions (i.e. wing pattern). We explicitly acknowledge the need of an integrative approach combining morphological and molecular data in the future (Padial et al. 2010). It is obvious that many of our taxonomic decisions need to be corroborated by (more) morphological data. However, we believe that providing an updated taxonomy (with the possibility that some conclusions will later be rejected) has by far more advantages than drawbacks, and hopefully will stimulate more research on poorly studied taxa. For example, it is more definite and concise to refer in future works to "Erebochlorini" than to an "unnamed Larentiinae clade comprising the genera *Erebochlora* Warren, 1895, *Cirrolygris* Warren, 1895, and *Deinoptila* Warren, 1900".

Proposed changes to the current classification are explicitly stated and summarized in a table for three affected subfamilies. In this paper, we propose: 1) new tribes, 2) new tribe synonymies, 3) new tribe assignments, 4) new genus-level synonymies, 5) new combinations, and 6) genera listed – ad interim – in quotation marks. The latter includes the exclusion of a species from its current combination. For example, many Chilean species were originally (or later) assigned to Palaearctic or Holarctic genera. We follow the practice used e.g. by Scoble (1999) and Pitkin (2002) and put doubtful genus combinations into quotation marks.

Results and Discussion are given at the subfamily level in the following order: Sterrhinae, Larentiinae, Archiearinae, Desmobathrinae, Oenochrominae, Geometrinae, Ennominae, and within subfamilies, taxa are treated in the order of the tree derived from IQ-TREE analysis (Electronic Supplement Files 1 and 2).

3. Results

In this section, we present a short overview of the results, including all tables and figures. See Murillo-Ramos et al. (2019) for a more detailed overview. In order to avoid redundancy, detailed results are presented and discussed together in the next section. Results of both the IQ-TREE analyses (Electronic Supplement Files 1 and 2) and the RAxML analyses (Murillo-Ramos et al. 2019) are very similar with only a few exceptions. Neotropical taxa are found throughout the topology, with several larger radiations in South America. **Sterrhinae**: See Fig. 1 for an overview at the tribe level and Electronic Supplement Files 1 and 2. Specimens are illustrated in Electronic Supplement File 3. **Larentiinae**: Our analyses show a large number of new, well-supported, tribe level clades which are discussed in detail in the Discussion section. See Fig. 2 for an overview at the tribe level, Fig. 3 for images of adult moths and Electronic Supplement Files 1 and 2. Specimens are illustrated in Electronic Supplement File 4. Taxonomic changes in Larentiinae are summarized in Table 1. **Geometrinae**: See Fig. 4 for an overview at the tribe level and Electronic Supplement Files 1 and 2. Specimens are illustrated in Fig. 5 and Electronic Supplement File 3. Taxonomic changes in Geometrinae are summarized in Table 2. **Ennominae**: See Fig. 6 for an overview at the tribe level, Fig. 7 for images of adult moths and Electronic Supplement Files 1 and 2. All analysed specimens are illustrated in Electronic Supplement File 5. Taxonomic changes in Ennominae are summarized in Table 3. Small subfamilies **Archiearinae**, **Oenochrominae**, **Desmobathrinae**, **Epidesmiinae**: See Electronic Supplement Files 1 and 2. Specimens are illustrated in Electronic Supplement File 3.

4. Discussion

4.1. Sterrhinae Meyrick, 1892

See Fig. 1 for phylogenetic relationships.

Sterrhinae will be dealt with in detail by Sihvonen et al. (accepted), they are not illustated in the text and the discussion of this subfamily is therefore kept to a minimum. The genera *Almodes* Guenée, [1858], *Ametris* Hübner,

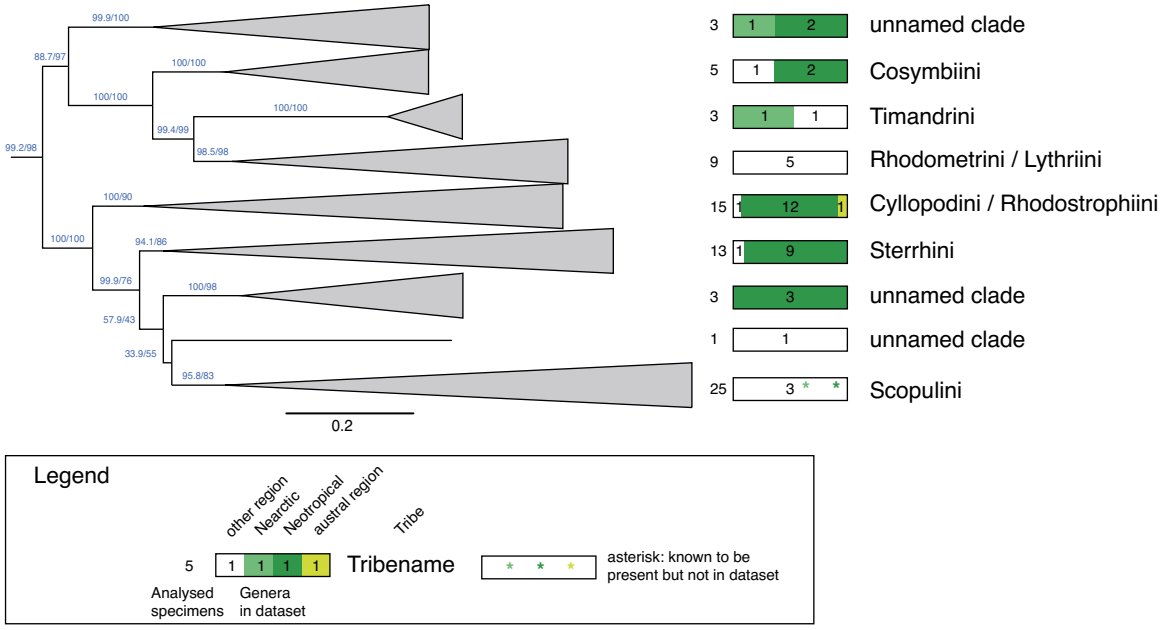

Fig. 1. Sterrhinae tribe composition. Tribes with New World representatives marked in colour: light green Nearctic, dark green Neotropical, yellowish green austral region. Support values in blue colour (SH-like and UFBoot values).

[1822], *Ergavia* Walker, 1866, and *Macrotes* Westwood, 1841 will be transferred from Oenochrominae to Sterrhinae in the revived tribe Mecoceratini (Sihvonen et al. accepted). Existing tribe assignments of New World taxa are supported in most cases in Cosymbiini, Sterrhini and Scopulini. *Pseudasellodes* Warren, 1904 (not assigned to tribe so far) is sister to *Proutoscia* Schaus, 1912. Remarkably, "*Lophochorista*" *porioni* Herbulot, 1988 is not a Geometrinae but belongs to a larger Neotropical clade within the tribe Sterrhini. The association of "*Lophochorista*" *porioni* with Sterrhinae was already suggested by Scoble (1999), questioning Herbulot's generic combination. Our data suggest that two genera currently assigned to Cosymbiini (*Hemipterodes* Warren, 1906 and *Lipotaxia* Prout, 1918) also belong to Sterrhini clade. Furthermore, our data indicate that yellow-black coloration has evolved potentially three times independently in diurnal Neotropical Sterrhinae. *Xanthyris* Felder & Felder, 1862 is not closely related to the other two investigated Cyllopodini genera *Atyria* Hübner, 1823 and *Smicropus* Warren, 1895. Support for a sister group relationship between *Atyria* and *Smicropus* is poor in the RAxML analysis (Murillo-Ramos et al. 2019), and the two genera even fall into different parts of the IQ-TREE analysis.

4.2. Larentiinae Duponchel, 1845

See Fig. 2 for phylogenetic relationships, Fig. 3 for habitus pictures of exemplary species, and Table 1 for proposed taxonomic changes.

Our study focuses on the tribe composition and formal taxonomic changes required for a natural system of the subfamily. Such changes include both New and Old World taxa. The relationships within the subfamily will be discussed in more detail by E. Õunap et al. (in prep.).

4.2.1. Dyspteridini. The tribe was revived by Viidalepp (2011) from synonymy with Trichopterygini. The position of Dyspteridini as sister to all other studied Larentiinae is confirmed (Strutzenberger et al. 2010; Sihvonen et al. 2011; Õunap et al. 2016). Sihvonen et al. (2011) found a close relationship of Neotropical *Dyspteris* Hübner, 1818 (Fig. 3A), and the New Zealand genus *Paradetis* Meyrick, 1885, confirmed by Õunap et al. (2016) and our study. Our analysis confirms a close relationship of European *Celonoptera* Lederer, 1862 with *Dyspteris* which was already suspected by early authors (cited in Õunap et al. 2016). *Celonoptera*, *Heterophleps* Herrich-Schäffer, [1854] and *Chlorotimandra* Butler, 1882, are formally transferred to Dyspteridini (Table 1). Since apart from the type species, almost all other members of *Heterophleps* occur in Asia, the monophyly and tribe assignment of Asian species combined to this genus need to be investigated in future studies.

4.2.2. Brabirodini Brehm, Murillo-Ramos & Õunap, new tribe. — **Type genus.** *Brabirodes* Warren, 1904 (Fig. 3B). — **Material examined and phylogeny.** *Brabirodes cerevia peruviana* Warren, 1904. *Brabirodes* forms a distinct lineage of Larentiinae which is sister to the rest of the subfamily, except Dyspteridini. Branch support values from the IQ-TREE analyses strongly confirm the sister-relationship to all other Larentiinae with the exception of Dyspteridini (SH-like = 83.5, UFBoot2 = 83). — **Molecular evidence.** The tribe is characterized by DNA sequence data from the following five gene regions (voucher gb-ID-19269, *Brabirodes cerevia*, from Ecuador, illustrated in Electronic Supplement File 5): ArgK

(MK738419), COI (MK739303), EF1a (MK739881), MDH (MK741089), Nex9 (MK741532). — **Morphology.** *Brabirodes* superficially resembles *Eupithecia* species (and is sometimes found in collections among *Eupithecia*). *Brabirodes* can be diagnosed by large and extremely elongated forewings, hindwings are small with undulating margin, anal area of male hindwing is without fold, and male antennae are bipectinate. Male genitalia are illustrated in Viidalepp (2011). Combination of these characters differentiates it from Dyspteridini and Trichopterygini (see Viidalepp 2011 for details).

4.2.3. Trichopterygini. Our results confirm the finding that Trichopterygini and Chesiadini are not sister taxa (Õunap et al. 2016). However, the position of these tribes has switched in our analysis compared to previous studies, meaning that Trichopterygini have branched off from the main lineage Larentiinae earlier than Chesiadini. While tribe assignment is confirmed in most cases, there are four formal new tribe assignments of New World genera: *Aloba* Warren, 1895, *Anomozela* Fletcher, 1979 (Fig. 3C), *Isosauris* Warren, 1894, and *Synpelurga* Butler, 1882 are transferred to Trichopterygini (Table 1). *Lobidiopteryx* Warren, 1902 was treated by Prout (1929–1935) as "one of the few African representatives of the *Lobophora* group of genera", with the Old World genus *Episteira* Warren, 1899 being listed almost immediately after it. The former "*Lobophora* group" has subsequently been changed to Lobophorini, and then synonymized with Trichopterygini (Õunap et al. 2016). We formally transfer the two genera as well as New Zealandian *Tatosoma* Butler, 1874 to Trichopterygini (Table 1), as earlier suggested by Dugdale (1980) and Õunap et al. (2016). Moreover, an undescribed genus (voucher PS225 from South Africa) also belongs to this tribe.

4.2.4. Chesiadini. Analysed specimens currently comprise three Palaearctic samples (genera *Aplocera* Stephens, 1827, and *Chesias* Treitschke, 1825), but none of our New World samples falls into this tribe. Currently, several New World species are assigned to *Lithostege* Hübner, [1825]. None of the Nearctic species belongs to *Lithostege* (B.C.S., unpubl. data), and it needs to be established whether any of the Neotropical species are actually congeneric with the Palaearctic type species of the genus.

4.2.5. Chrismopterygini Brehm, Murillo-Ramos & Õunap, new tribe. — **Type genus.** *Chrismopteryx* Prout, 1910 (Fig. 3D). — **Material examined and phylogeny.** The clade comprises *Chrismopteryx politata* Fletcher, 1953, an unidentified *Chrismopteryx* species, "*Nebula*" *pseudohalia* (Butler, 1882), and "*Anticlea*" *oculisigna* Prout, 1923. Branch support values from the IQ-TREE analyses clearly confirm the monophyly of this clade (SH-like = 99.9, UFBoot2 = 100). — **Molecular evidence.** The tribe is characterized by DNA sequence data from the following seven gene regions (exemplar *C. politata*, voucher bo_chi_120 from Chile, illustrated in Fig. 3D): ArgK (MK738169), CAD (MK738909), COI (MK739064), EF1a (MK739699), GADPH (MK740314), Nex9 (MK741346), Wingless (MK742140). — **Morphology.** Delicately built species. Forewings wide, postmedial line often undulating, medial area often weakly darkened. Hindwings with weak markings or markings absent. External features of analysed species are illustrated in Fig. 3D and Electronic Supplement File 4. — **Remarks and taxonomic changes.** *Psaliodes pseudohalia* Butler, 1882 is transferred from *Nebula* to *Chrismopteryx* (**comb.n.**) (Table 1). All other Chilean "*Nebula*" species are excluded from the genus (Table 1). Since "*Anticlea*" *oculisigna* Prout, 1923 [1855] is misplaced, the genus should be listed – ad interim – with quotation marks (Table 1); the type species of *Anticlea* Stephens, 1831 (Larentiini) is Palaearctic. Immature stages of *Chrismopteryx undularia* (Blanchard, 1852) are described in Vargas et al. (2010).

4.2.6. Eudulini. Our results confirm the phylogenetic position of the tribe as presented by Õunap et al. (2016). They showed that the New World genera *Eubaphe* Hübner, 1823, and *Eudulophasia* Warren, 1897, form a well supported clade. Our analysis now also includes *Eudule* Hübner, 1823, and it shows that the three genera are closely related. Our results also suggest that the Neotropical genera *Graphidipus* Herrich-Schäffer, [1855] (Fig. 3E) and *Crocypus* Herrich-Schäffer, [1855] form a lineage sister to this clade, and can thus be formally integrated into the Eudulini (Table 1, Electronic Supplement File 4).

4.2.7. Asthenini. This tribe is represented only by relatively few taxa in the New World, namely the Holarctic *Hydrelia* Hübner, [1825] and *Venusia* Curtis, 1839 (with Palaearctic species in the analysis). The only known genus of this tribe occurring in the Neotropical region is *Eois* (Fig. 3F) – but with more than 200 described and many more undescribed species (Brehm et al. 2011) probably outnumbering all other taxa of this tribe in terms of species richness. Phylogenetic relationships within the Asthenini were already reported by Sihvonen et al. (2011) and are supported by further analyses (e.g. Õunap et al. 2016).

4.2.8. Perizomini. Our analysis only comprises material sampled in Europe: the type species of *Perizoma* Hübner, [1825], *P. albulata* ([Denis & Schiffermüller], 1775); three more species of *Perizoma*, and one species of *Mesotype* Hübner, [1825]. Probably none of the native North American "*Perizoma*" species is congeneric with true *Perizoma* – *P. alchemillata* (Linnaeus, 1758) has been introduced to North America from Europe – and it is possible that the tribe is naturally not present at all in the New World (B.C.S., unpublished). All other sampled "*Perizoma*" species belong to other tribes (for details see 4.2.14. Psaliodini, 4.2.18. Scotopterygini, 4.2.20.2. Larentiini, 4.2.20.4 Ennadini). *Perizoma* has thus been a Larentiinae "trash bin", and it seems likely that even

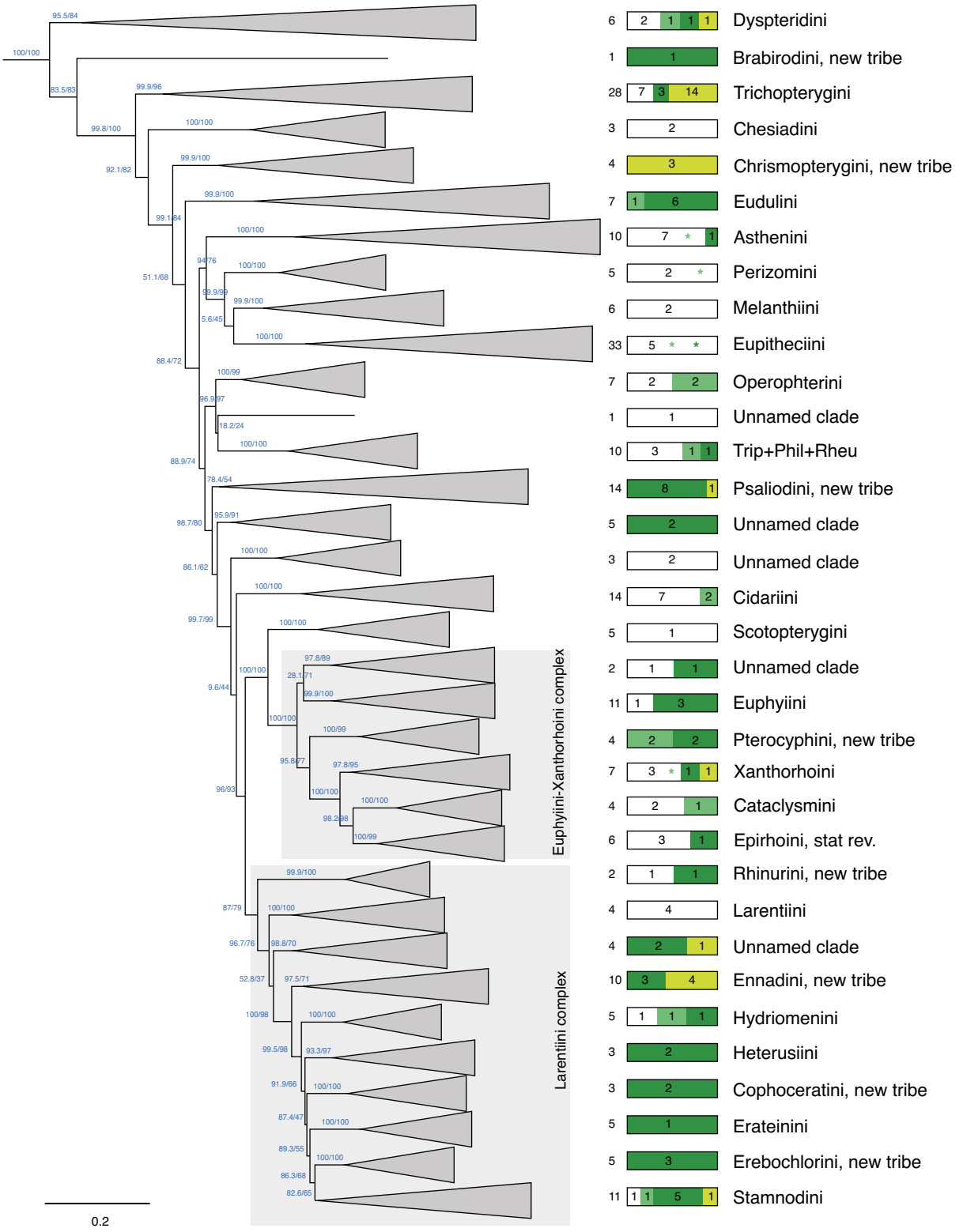

Fig. 2. Larentiinae tribe composition. Tribes with New World representatives marked in colour: light green Nearctic, dark green Neotropical, yellowish green austral region; see also explanatory box in Fig. 1. Trip+Phil+Rheu: Triphosini + Phileremini + Rheumapterini clade. Support values in blue colour (SH-like and UFBoot values).

more lineages were assigned to the genus, e.g. species around *P. fallax* Warren, 1905. Similar results have also been shown by Õunap et al. (in press). We conclude that it is very likely that all New World species assigned to *Perizoma* are probably misplaced, and we therefore suggest to list the genus – ad interim – with quotation marks for all its Neotropical species (Table 1). An integrative revision of the genus is required to provide new nomenclatorial combinations – and to clean this "Larentiinae trash bin".

4.2.9. Melanthiini. Our data only comprises material sampled in Europe and Africa (several species of *Horisme* Hübner, [1825], and the type species of *Melanthia* Duponchel, 1829). Only a few *Horisme* species occur in the New World, and their assignment needs to be checked in future studies.

4.2.10. Eupitheciini. Our phylogeny currently comprises no New World samples. However, the globally most species-rich genus *Eupithecia* Curtis, 1825, is also one of the most species-rich genera in North America (Bolte 1990), and the Andes are possibly even the most species-rich region in the world for *Eupithecia* (Brehm et al. 2016) where it shows remarkable morphological diversification (Herbulot 2001).

4.2.11. Operophterini. Our analysis comprises the Holarctic genera *Operophtera* Hübner, [1825], *Malacodea* Tengström, 1869, and *Epirrita* Hübner, 1822. We are not aware of the presence of Operophterini in the Neotropical region.

4.2.12. Solitaneini. *Baptria* Hübner, [1825] is an enigmatic genus currently assigned to the tribe Solitaneini based on morphology (Hausmann & Viidalepp 2012). The phylogenetic position of *Solitanea* Djakonov, 1924 and Solitaneini needs to be tested in future studies (Õunap et al. 2016).

4.2.13. Clade Triphosini + Phileremini + Rheumapterini. A close relationship of these tribes has been recognized before (e.g., Õunap et al. 2016; Schmidt 2017) – and a synonymization could be considered in future works. Our representatives of New World *"Triphosa"*, and the type species of *Coryphista* Hulst, 1896 fall into the Rheumapterini, very close to *Rheumaptera* Hübner, 1822. We regard monotypic *Coryphista* as a junior synonym of *Rheumaptera* (Table 1). *Scotosia pallidividata* Snellen, 1874 is transferred from *Triphosa* Stephens, 1829 to *Rheumaptera* (**comb.n.**) (Fig. 3G), and *Scotosia affirmata* Guenée, [1858] is transferred from *Triphosa* to *Rheumaptera* (**comb.n.**) (Table 1, illustrated in Electronic Supplement File 4). The generic placement of further New World species currently assigned to *Triphosa* need to be investigated in future studies.

4.2.14. Psaliodini Brehm, Murillo-Ramos & Õunap, new tribe. — **Type genus.** *Psaliodes* Guenée, [1858] (Fig. 3H). — **Material examined and phylogeny.** *Psaliodes* near *planiplaga* Warren, 1904 clusters with *P. prunicolor* (Warren, 1904), and the two taxa are sister to *Distoneura pastaza* (Prout, 1934). Only Psaliodini s.str. has high support values from the IQ-TREE analyses (SH-like = 99.9, UFBoot2 = 100) whereas branch support values of Psaliodini s.l. are weaker (SH-like = 78.4, UFBoot2 = 54), The assignment of the genera *Anthalma* Warren, 1901, *Plemyriopsis* Warren, 1895, and *Smileuma* Prout, 1910 to Psaliodini therefore requires further scrutiny. — **Molecular evidence.** The tribe is characterized by DNA sequence data from the following six gene regions (exemplar *Psaliodes* near *planiplaga*, voucher gb-CR-S-1708 from Costa Rica, illustrated in Electronic Supplement File 5) CAD (JF785161), COI (JF784674), EF1a (JF785299), IDH (JF785474), MDH (JF784818), Wingless (JF785049). Our analysis includes *Psaliodes* near *planiplaga* which is – judged from wing morphology – closely related with *P. flavagata* Guenée [1858], the type species of *Psaliodes* (Electronic Supplement File 4). *Distoneura* Fletcher, 1979, is the second genus that can safely be assigned to Psaliodini. Further phylogenetic studies should establish whether this genus is sister to or nested within the species-rich genus *Psaliodes*. — **Morphology.** External features of analysed species are illustrated in Fig. 3H and Electronic Supplement File 4. Further detailed morphological analysis is required to identify potential diagnostic features. — **Remarks and taxonomic changes.** One clade comprises "*Monarcha*" (Scoble 1999: no published reference found; apparently preoccupied in Aves: *Monarcha* Vigors & Horsfield, 1827) and "*Psaliodes*" *picta* Warren, 1904. Another clade comprises three unidentified species of *Anthalma* Warren, 1901 and "*Euphyia*" *balteata* (Warren, 1905) (wrong generic placement: see below). Another clade includes *Plemyriopsis* and *Smileuma* Prout, 1910, another includes "*Nebula*" *cynthia* (Butler, 1882), "*Nebula*" near *emilia* (Butler, 1882) and "*Euphyia*" *psyroides* Warren, 1897 **stat.rev.** (from Peru) which we revive from synonymy with "*Euphyia*" *psyra* Druce, 1883 (from Guatemala) (Table 1). A strange coincidence is that Herbulot described *Epirrhoe psyroides* Herbulot, 1988 from Bolivia which appears to be the same species as *psyroides* Warren (all taxa illustrated in Electronic Supplement File 4). Herbulot's taxon would be a junior homonym of Warren's taxon only once the two taxa are combined with a nomenclaturally available (new) genus name in future studies. For erroneous placement of Chilean "*Nebula*", see also Chrismopterygini and Ennadini. Since "*Epirrhoe*" *psyroides* Herbulot, 1988 is not related to true *Epirrhoe* (see Epirrhoini), the genus should be listed – ad interim – with quotation marks (Table 1). All species are illustrated in Electronic Supplement File 5. Because of their wing morphology, the species *Cidaria bogotata* Walker, 1862 and *Plerocymia rhombifascia* Warren, 1905 are transferred from *Perizoma* to *Smileuma* (**comb.n.**) (Table 1, illustrated in Electronic Supplement File 4). "*Psaliodes*" *picta* should be listed – ad interim – with quotation marks (see true *Psaliodes* in Psaliodini) because it is not in the same subclade as *Psaliodes* near *planiplaga*. P. Strutzenberger et al. will revise the *Psaliodes* group (including "*Monarcha*" *magicaria* Felder & Rogenhofer, 1875) and will revive *Alydda* Walker, 1861 with subsequent new nomenclatorial combinations. *Orthoprora balteata* Warren, 1905 is transferred from *Euphyia* Hübner, [1825] to *Anthalma* (**comb.n.**) and *Rhopalodes parecida* Dognin, 1892 is transferred from *Rhopalodes* to *Anthalma* (**comb.n.**) (Table 1). Because of their wing morphology, twelve further species are transferred to *Anthalma*, either from *Euphyia* or *Perizoma* (Table 1, illustrated in Electronic Supplement File 4).

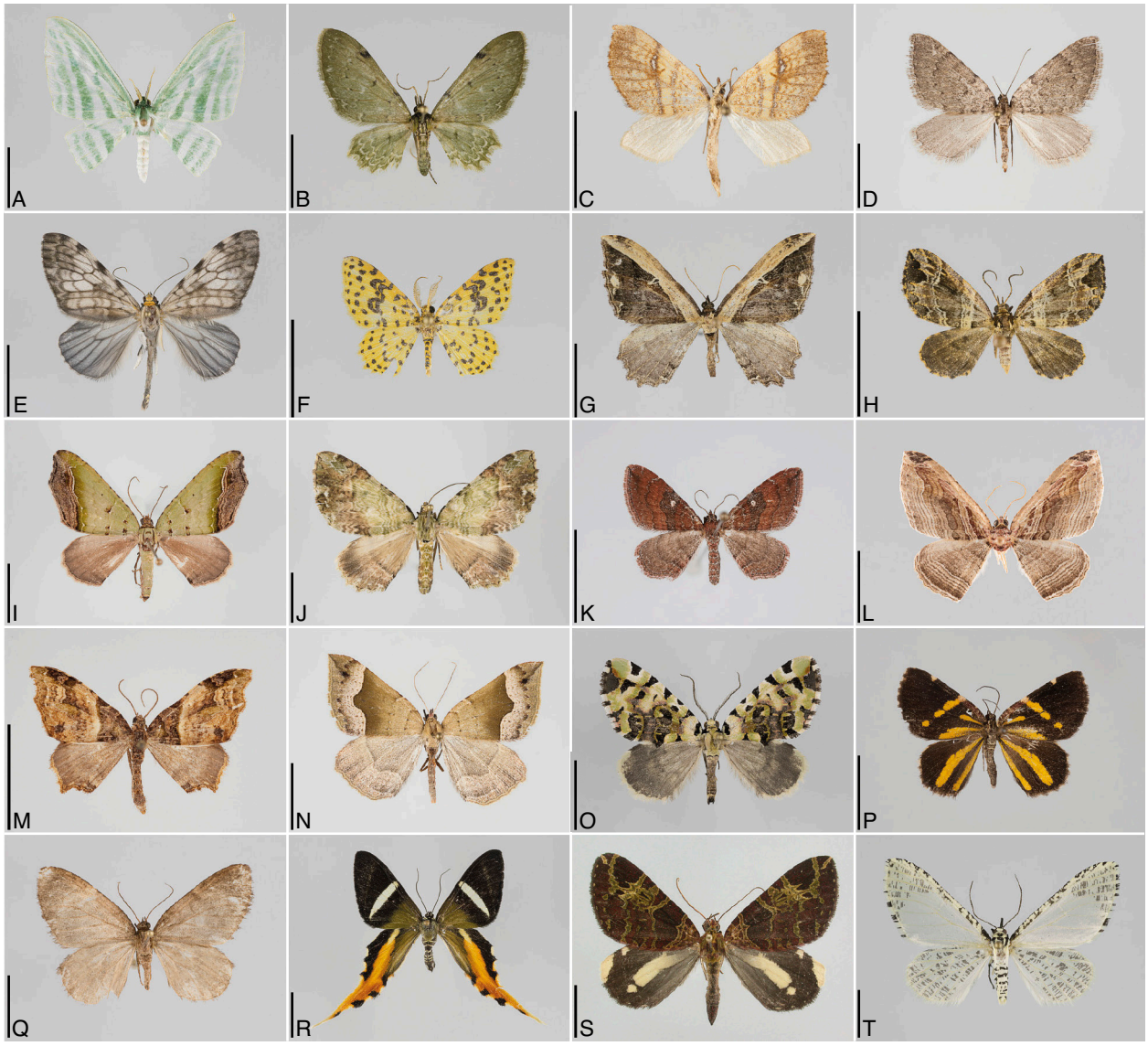

Fig. 3. Illustrations of selected Neotropical Larentiinae taxa. **A**: Dyspteridini, *Dyspteris* sp. (Pe-Geo-0205). **B**: Brabirodini, **new tribe**, *Brabirodes cerevia peruviana* Warren, 1904 (Pe-Geo-0495). **C**: Trichopterygini, *Anomozela cirrhiata* (Felder & Rogenhofer, 1875) (Ch-Geo-0009). **D**: Chrismopterygini, **new tribe**, *Chrismopteryx politata* Fletcher, 1953 (bo_chi_120). **E**: Eudulini, *Graphidipus pilifera* (Dognin, 1912) (Pe-Geo-0621). **F**: Asthenini, *Eois* near *golosata* (Dognin, 1893) (Pe-Geo-0119). **G**: Rheumapterini, *Rheumaptera pallidivittata* (Snellen, 1874) **comb.n.** (Pe-Geo-0039). **H**: Psaliodini, **new tribe**, *Psaliodes* near *tripartita* (Warren, 1904) (Pe-Geo-0199). **I**: Euphyiini, *Oligopleura malachitaria* (Herrich-Schäffer, [1855]) (Pe-Geo-0012). **J**: Pterocyphini, **new tribe**, *Pterocypha gibbosaria* Herrich-Schäffer, [1855] (Br-Geo-059). **K**: Xanthorhoini, *Orthonama* near *plemyrata* (Felder & Rogenhofer, 1875) (GB_Geo_068). **L**: Epirrhoini, **revived tribe**, "*Euphyia*" *sturnularia* Herrich-Schäffer, [1855] (EO1180). **M**: Rhinurini, **new tribe**, *Rhinura variegata* (Warren, 1901), synonym of *R. populonia* (Druce, 1893) (type specimen in NHM, London). **N**: Ennadini, **new tribe**, *Ennada pellicata* (Felder & Rogenhofer, 1875) (Ch-Geo-0010). **O**: Hydriomenini, *Ersephila prema* Druce, 1893 (Gu_Geo_006). **P**: Heterusiini, *Heterusia quadruplicaria* (Geyer, 1832) (AH7173). **Q**: Cophoceratini, **new tribe**, *Cophocerotis costinotata* (Warren, 1908) (gb-ID-19302). **R**: Erateinini, *Erateina drucei* (Thierry-Mieg, 1893) (Pe-Geo-0534). **S**: Erebochlorini, **new tribe**, *Erebochlora* near *tesserulata* Felder & Rogenhofer, 1875 (gb-CR-S-1218). **T**: Stamnodini: *Callipia anthocharidaria* (Oberthür, 1881) **comb.n.** (Pe-Geo-0804).

4.2.15. Unnamed clade. This entirely Neotropical clade comprises a species that is apparently undescribed and that cannot be assigned to a genus, and four species of *Perizoma* that are hereby excluded from *Perizoma*, i.e. the taxa *vireonaria* Maassen, 1890, *cretinotata* Bastelberger, 1907, *versatilis* Dognin, 1911 and *cyrtozona* Prout, 1922 (Table 1). As judged by wing morphology, "*Perizoma*" *amplata* Warren, 1904 and "*Perizoma*" *mirifica* Warren, 1904 also belong to this clade (illustrated in Electronic Supplement File 4). This *amplata*-group probably requires the establishment of a new genus which is beyond the scope of this study.

4.2.16. Unnamed clade. This well supported clade (SH-like = 100, UFBoot2 = 100) comprises *Lampropteryx* Stephens, 1831 and *Coenotephria* Prout, 1914. Both genera are mainly distributed in the Old World, although *Lampropteryx suffumata* ([Denis & Schiffermüller], 1775) is also naturally Holarctic (deWaard et al. 2008). In the analysis by Õunap et al. (2016), this clade was the basal-

Table 1. Taxonomic changes in Larentiinae at the level of tribes, genera and species, in alphabetical order. *Old World taxa.

Revived tribes	**Included taxa**
Epirrhoini **stat. rev.**	*Epirrhoe* Hübner, [1825], *Catarhoe* Herbulot, 1951, *Mimoclystia* Warren, 1901, *Euphyia sturnularia* Herrich-Schäffer, [1855]
New tribes	**Included taxa**
Brabirodini **new tribe**	*Brabirodes* Warren, 1904
Chrismopterygini **new tribe**	*Chrismopteryx* Prout, 1910
Cophoceratini **new tribe**	*Cophocerotis* Warren, 1895, *Hagnagora* Druce, 1885
Ennadini **new tribe**	*Ennada* Blanchard, 1852, *Spargania* Guenée, [1858], several unnamed genera
Erebochlorini **new tribe**	*Erebochlora* Warren, *Cirrolygris* Warren, 1895, *Deinoptila* Warren, 1900
Pterocyphini **new tribe**	*Pterocypha* Herrich-Schäffer, [1855], *Obila* Walker, 1869, *Archirhoe* Herbulot, 1951
Psaliodini **new tribe**	*Psaliodes* Guenée, [1858], *Distoneura* Fletcher, 1979
Rhinurini **new tribe**	*Rhinura* Warren, 1904, *Haplolabida* Fletcher, 1958*, *Urocalpe* Warren, 1904
Revived genera	**Was in synonymy with; included species**
Synneuria Mabille, 1885 **stat. rev.**	*Stamnodes* Guenée, [1858]; *Synneuria camposi* Orfila & Schajovski, 1964, *Synneuria carcavalloi* Orfila & Schajovski, 1962, *Synneuria ditissima* Thierry-Mieg, 1904
Revived species	**Was in synonymy with**
Euphyia psyroides Warren, 1897 **stat. rev.**	*Euphyia psyra* Druce, 1883
Synonymized genera	**Valid genus**
Anemplocia Warren, 1905 **syn.n.**	*Erateina* Doubleday, 1848
Coryphista Hulst, 1896 **syn.n.**	*Rheumaptera* Hübner, 1822
Cyclica Grote, 1882 **syn.n.**	*Hydriomena* Hübner, [1825]
Priapodes Warren, 1895 **syn.n.**	*Erebochlora* Warren, 1895
„*Trocherateina*" Prout, 'no published reference' (Fletcher 1979)	*Erateina* Doubleday, 1848
New generic combinations	**Originally described in genus, transferred from genus, decision based on**
Anthalma alboscripta (Dognin, 1892) **comb.n.**	*Cidaria*, *Euphyia*, external morphology
Anthalma apicesignata (Dognin, 1913) **comb.n.**	*Perizoma*, external morphology
Anthalma arcillata (Dognin, 1893) **comb.n.**	*Cidaria*, *Perizoma*, external morphology
Anthalma artemas (Schaus, 1912) **comb.n.**	*Anapalta*, *Euphyia*, external morphology
Anthalma balteata (Warren, 1905) **comb.n.**	*Orthoprora*, *Euphyia*, molecular data and external morphology
Anthalma cortada (Dognin, 1893) **comb.n.**	*Cidaria*, *Euphyia*, external morphology
Anthalma cortatoides (Dognin, 1893) **comb.n.**	*Cidaria*, *Euphyia*, external morphology
Anthalma parecida (Dognin, 1892) **comb.n.**	*Lobophora?*, *Rhopalodes*, external morphology
Anthalma plumbeipennis (Dognin, 1914) **comb.n.**	*Orthoprora*, *Euphyia*, external morphology
Anthalma curviviata (Dognin, 1914)	*Euphyia*, external morphology
Anthalma rojiza (Dognin, 1893) **comb.n.**	*Cidaria*, *Euphyia*, external morphology
Anthalma terminisecta (Dognin, 1914) **comb.n.**	*Anapalta*, *Euphyia*, external morphology
Anthalma zara (Thierry-Mieg, 1893) **comb.n.**	*Cidaria*, *Euphyia*, external morphology
Callipia anthocharidaria (Oberthür, 1881) **comb.n.**	*Larentia*, *Stamnodes*, molecular data and external morphology
Chrismopteryx pseudohalia (Butler, 1882) **comb.n.**	*Psaliodes*, *Nebula*, molecular data and external morphology
Euphyia tricolorata (Dognin, 1902) **comb.n.**	*Ochyria*, *Xanthorhoe*, molecular data and external morphology
Smileuma bogotata (Walker, 1862) **comb.n.**	*Cidaria*, *Perizoma*, external morphology
Smileuma rhombifascia (Warren, 1905) **comb.n.**	*Plerocymia?*, *Perizoma*, external morphology
Rheumaptera pallidivittata (Snellen, 1874) **comb.n.**	*Scotosia*, *Triphosa*, molecular data and external morphology
Rheumaptera affirmata (Guenée, [1858]) **comb.n.**	*Scotosia*, *Triphosa*, molecular data and external morphology
Scotopteryx bitrita (Felder & Rogenhofer, 1875)* **comb.n.**	*Ortholitha*, *Larentia*, molecular data
Scotopteryx epipercna (Wehrli, 1931)* **comb.n.**	*Onychia*, *Perizoma*, molecular data
Orthonama inflexa (Dognin, 1914) **comb.n.**	*Coenocalpe*, *Scotopteryx*, external morphology
Spargania coeruleopicta Warren, 1908 **comb.n.**	*Perizoma*, external morphology
Spargania emmelesiata (Snellen, 1874) **comb.n.**	*Cidaria*, *Perizoma*, external morphology
Spargania zenobia (Thierry-Mieg, 1893) **comb.n.**	*Cidaria*, *Perizoma*, molecular data and external morphology
Tribe changes	**Genus**
Hydriomenini to Cidariini	*Ceratodalia* Packard, 1876

Table 1 continued.

Trichopterygini to Dyspteridini	*Celonoptera* Lederer, 1862*
Trichopterygini to Dyspteridini	*Heterophleps* Herrich-Schäffer, [1854]
unassigned to Dyspteridini	*Chlorotimandra* Butler, 1882
unassigned to Trichopterygini	*Aloba* Warren, 1895
unassigned to Ennadini	"*Hagnagora*" *mesenata* Felder & Rogenhofer, 1875
unassigned to Eudulini	*Graphidipus* Herrich-Schäffer, [1855]
unassigned to Eudulini	*Crocypus* Herrich-Schäffer, [1855]
unassigned to Heterusiini	*Spiloctenia* Warren, 1897
unassigned to Trichopterygini	*Anomozela* Fletcher, 1979
unassigned to Trichopterygini	*Isosauris* Warren, 1894
unassigned to Trichopterygini	*Synpelurga* Butler, 1882
unassigned to Trichopterygini	*Tatosoma* Butler, 1874*
unassigned to Trichopterygini	*Lobidiopteryx* Warren, 1902*
unassigned to Trichopterygini	*Episteira* Warren, 1899*
unassigned to Stamnodini	*Pseudopsodos* Thierry-Mieg, 1903
unassigned to Stamnodini	*Scordyliodes* Thierry-Mieg, 1903
Xanthorhoini to Cataclysmini	*Zenophleps* Hulst, 1896
Species proposed to be excluded from genera = incertae sedis	**Tribe assignment, country, originally described in**
"*Anticlea*" *oculisigna* (Prout, 1923) (analysed)	Chrismopterygini, Argentina, *Larentia*
"*Anticlea*" *badiiplaga* (Fletcher, 1953) (not analysed)	unknown, Argentina, *Earophila*
"*Anticlea*" *chillanensis* (Butler, 1882) (type image checked)	unknown, Chile, *Larentia*
"*Anticlea*" *crepusculata* (Fletcher, 1953) (not analysed)	unknown, Argentina, *Earophila*
"*Epirrhoe*" *psyroides* Herbulot, 1988 (analysed)	Plemyriopsini, Bolivia, *Epirrhoe*
"*Heterusia*" *picata* Dognin, 1904 (analysed)	unnamed tribe, Ecuador, *Heterusia*
"*Heterusia*" *plagia* (Druce, 1893) (analysed)	unnamed tribe, Ecuador, *Trochiodes*
"*Heterusia*" *adventa* Prout, 1934 (type image checked)	Ennadini, Argentina, *Scordylia*
"*Heterusia*" *barrioso* Ureta, 1956 (type image checked)	Ennadini, Chile, *Heterusia*
"*Nebula*" *adela* (Butler, 1893) (type image checked)	unknown, Chile, *Cidaria*
"*Nebula*" *aleucidia* (Butler, 1882) (type image checked)	Plemyriopsini, Chile, *Cheimatobia*
"*Nebula*" *bellissima* (Butler, 1893) (not analysed)	unknown, Chile, *Spargania*
"*Nebula*" *corticalis* (Butler, 1882) (type image checked)	unknown, Chile, *Anticlea*
"*Nebula*" *ceres* (Butler, 1882) (type image checked)	unknown, Chile, *Cidaria*
"*Nebula*" *cylon* (Druce, 1893) (type image checked)	unnamed lineage, Mexico, *Hammaptera*
"*Nebula*" *cynthia* (Butler, 1882) (analysed)	unnamed lineage, Chile, *Cidaria*
"*Nebula*" *decipiens* (Butler, 1882) (type image checked)	unnamed lineage, see *emilia*
"*Nebula*" *detritaria* (Staudinger, 1899) (not analysed)	unknown, Chile, *Coremia*
"*Nebula*" *diana* (Butler, 1882) (type image checked)	unnamed lineage, Chile, *Cidaria*
"*Nebula*" *dubia* (Butler, 1882) (type image checked)	unknown, Chile, *Camptogramma*
"*Nebula*" *emilia* (Butler, 1882) (analysed)	unnamed lineage, Chile, *Cidaria*
"*Nebula*" *flexuosa* (Dognin, 1914) (type image checked)	unknown, Colombia, *Anticlea*
"*Nebula*" *ignipennis* (Butler, 1882) (type image checked)	Ennadini, Chile, *Ochyria*
"*Nebula*" *macidata* (Felder & Rogenhofer, 1875) (type image checked)	unknown, Chile, *Cidaria*
"*Nebula*" *mathewi* (Butler, 1883) (type image checked)	unknown, Chile, *Psaliodes*
"*Nebula*" *misera* (Butler, 1882) (type image checked)	unknown, Chile, *Cidaria*
"*Nebula*" *mutabilis* (Mabille, 1885) (not analysed)	unknown, Chile, *Cidaria*
"*Nebula*" *pusilla* (Butler, 1882) (type image checked)	unknown, Chile, *Chalastra?*
"*Perizoma*" *ablata* (Hulst, 1896) (not analysed)	unknown, USA, *Hydriomena*
"*Perizoma*" *actuata* (Pearsall, 1909) (not analysed)	unknown, USA, *Mesoleuca*
"*Perizoma*" *alaskae* (Hulst, 1896) (not analysed)	unknown, USA, *Coenocalpe*
"*Perizoma*" *amplata* Warren, 1904 (type image checked)	Plemyriopsini, *amplata*-group, Peru, *Perizoma*
"*Perizoma*" *alumna* (Prout, 1925) (analysed)*	Larentiini, South Africa, *Ortholitha*
"*Perizoma*" *anguliferata* (Maassen, 1890) (not analysed)	unknown, Bolivia, *Cidaria*
"*Perizoma*" *apiceflava* (Prout, 1910) (not analysed)	unknown, Peru, *Perizoma?*
"*Perizoma*" *aspersa* Dognin, 1904 (type image checked)	possibly Ennadini, Ecuador, *Perizoma*
"*Perizoma*" *aurantaria* (Jones, 1921) (not analysed)	unknown, Brazil, *Psaliodes*

Table 1 continued.

"*Perizoma*" *aureoviridis* Warren, 1904 (type image checked)	unknown, Peru, *Perizoma*
"*Perizoma*" *baptopennis* (Dyar, 1916) (type image checked)	unknown, Mexico, *Anapalta*
"*Perizoma*" *bogotata* (Walker, 1862) (type image checked)	unknown, Colombia, *Cidaria*
"*Perizoma*" *brunneopicta* Dognin, 1913 (type image checked)	unknown, Colombia, *Perizoma*
"*Perizoma*" *caeruleosecta* (Prout, 1916) (type image checked)	unknown, Peru, *Hammaptera*
"*Perizoma*" *carnepicta* Warren, 1905 (type image checked)	unknown, Peru, *Perizoma*
"*Perizoma*" *egena* (Bastelberger, 1911) (not analysed)	unknown, Peru, *Anapalta*
"*Perizoma*" *carnetincta* Dognin, 1911 (type image checked)	unknown, Colombia, *Perizoma*
"*Perizoma*" *cinereolimitata* (Thierry-Mieg, 1892) (type image checked)	unknown, Colombia, *Cidaria*
"*Perizoma*" *complicata* Dognin, 1911 (type image checked)	unknown, Colombia, *Perizoma*
"*Perizoma*" *constellata* Dognin, 1913 (type image checked)	unknown, Colombia, *Perizoma*
"*Perizoma*" *costiguttata* (Hulst, 1896) (not analysed)	unknown, USA, *Hydriomena*
"*Perizoma*" *cretinotata* Bastelberger, 1907 (analysed)	Plemyriopsini, *amplata*-group, Peru, *Perizoma*
"*Perizoma*" *curvisignata* Warren, 1909 (type image checked)	Plemyriopsini, *amplata*-group, Peru, *Perizoma*
"*Perizoma*" *curvilinea curvilinea* (Hulst, 1896) (not analysed)	unknown, Canada, *Hydriomena*
"*Perizoma*" *occidens* (Hulst, 1898) (not analysed)	unknown, USA, *Hydriomena*
"*Perizoma*" *curvilinea foxi* (Wright, 1924) (not analysed)	unknown, USA, *Venusia*
"*Perizoma*" *custodiata* (Guenee, [1858]) (not analysed)	unknown, USA, *Eubolia*
"*Perizoma*" *carnata* (Packard, 1874) (not analysed)	unknown, USA, *Phibalapteryx*
"*Perizoma*" *carneata* (Packard, 1876) (not analysed)	unknown, USA, *Ochyria*
"*Perizoma*" *gueneeata* (Packard, 1876) (not analysed)	unknown, USA, *Ochyria*
"*Perizoma*" *polygrammata* (Hulst, 1896) (not analysed)	unknown, USA, *Coenocalpe*
"*Perizoma*" *cyrtozona* Prout, 1922 (not analysed)	Plemyriopsini, *amplata*-group, Colombia, *Perizoma*
"*Perizoma*" *diltilla* (Dyar, 1913) (type image checked)	unknown, Peru, *Epirrhoe*
"*Perizoma*" *discors* (Warren, 1901) (type image checked)	unknown, Peru, *Epirrhoe?*
"*Perizoma*" *epictata* Barnes & McDunnough, 1916 (not analysed)	unknown, USA, *Perizoma*
"*Perizoma*" *eudoxia* Prout, 1934 (type image checked)	unknown, Colombia, *Perizoma*
"*Perizoma*" *fallax* Warren, 1905 (type image checked)	unknown, Peru, *Perizoma*
"*Perizoma*" *fractifascia* Dognin, 1911 (type image checked)	unknown, Colombia, *Perizoma*
"*Perizoma*" *grandis* (Hulst, 1896) (not analysed)	unknown, USA, *Eucymatoge*
"*Perizoma*" *grandis saawichata* (Swett, 1915) (not analysed)	unknown, Canada, *Hydriomena*
"*Perizoma*" *herrichiata* (Snellen, 1874) (not analysed)	unknown, Colombia, *Opisogonia*
"*Perizoma*" *iduna* Prout, 1910 (not analysed)	unknown, Argentina, *Perizoma?*
"*Perizoma*" *illimitata* Prout, 1922 (type image checked)	unknown, Peru, *Perizoma*
"*Perizoma*" *impromissata* (Walker, 1862) (type image checked)	unknown, Uruguay, *Ypsipetes?*
"*Perizoma*" *corticeata* (Walker, [1863]) (type image checked)	unknown, Uruguay, *Camptogramma*
"*Perizoma*" *fasciolata* Warren, 1897 (type image checked)	unknown, Paraguay, *Perizoma*
"*Perizoma*" *muscosata* Warren, 1900 (type image checked)	unknown, Argentina, *Perizoma*
"*Perizoma*" *ochritincta* Warren, 1905 (type image checked)	unknown, Mexico, *Perizoma*
"*Perizoma*" *puella* Prout, 1910 (not analysed)	unknown, unknown, *Perizoma*
"*Perizoma*" *interlauta* Warren, 1907 (not analysed)	unknown, Peru, *Perizoma*
"*Perizoma*" *mirifica* Warren, 1904 (not analysed)	Plemyriopsini, *amplata*-group, Peru, *Perizoma*
"*Perizoma*" *mixticolor* Dognin, 1913 (type image checked)	possibly Euphyiini, Colombia, *Perizoma*
"*Perizoma*" *mollis* Dognin, 1913 (type image checked)	unknown, *Eupithecia?*; Colombia, *Perizoma*
"*Perizoma*" *nigrostipata* Dognin, 1913 (type image checked)	unknown, Colombia, *Perizoma*
"*Perizoma*" *obtusa* (Warren, 1907) (type image checked)	unknown, Peru, *Opisogonia*
"*Perizoma*" *ochreata* (Grossbeck, 1910) (not analysed)	unknown, USA, *Mesoleuca*
"*Perizoma*" *oxygramma* (Hulst, 1896) (not analysed)	unknown, USA, *Coenocalpe*
"*Perizoma*" *tahoensis* Barnes & McDunnough, 1916 (not analysed)	unknown, USA, *Perizoma*
"*Perizoma*" *pastoralis* (Butler, 1882) (type image checked)	unknown, Chile, *Ypsipetes*
"*Perizoma*" *pecata* (Dognin, 1893) (type image checked)	unknown, Ecuador, *Cidaria*
"*Perizoma*" *perryi* Rindge, 1973 (not analysed)	unknown, Ecuador, *Perizoma?*
"*Perizoma*" *persectata* (Maassen, 1890) (type image checked)	unknown, Ecuador, *Cidaria*
"*Perizoma*" *plumbinotata* (Warren, 1904) (type image checked)	unknown, Peru, *Gagitodes*
"*Perizoma*" *pravata* (Dognin, 1900) (type image checked)	possibly Euphyiini, Bolivia, *Eucosmia*

Table 1 continued.

"*Perizoma*" *camptogrammaria* Warren, 1907 (not analysed)	unknown, Peru, *Perizoma*
"*Perizoma*" *quadriplaga* Dognin, 1911 (type image checked)	unknown, Colombia, *Perizoma*
"*Perizoma*" *renitens* Prout, 1910 (type image checked)	unknown, Peru, *Perizoma?*
"*Perizoma*" *rostrinotata* Dognin, 1913 (type image checked)	unknown, Colombia, *Perizoma*
"*Perizoma*" *sordescens* Dognin, 1908 (type image checked)	unknown, Peru, *Perizoma*
"*Perizoma*" *spilophylla* Prout, 1934 (type image checked)	unknown, Argentina, *Perizoma*
"*Perizoma*" *strictifascia* Warren, 1907 (type image checked)	unknown, Peru, *Perizoma*
"*Perizoma*" *tenuisecta* Prout, 1934 (type image checked)	unknown, Argentina, *Perizoma*
"*Perizoma*" *vacillans* (Warren, 1905) (type image checked)	unknown, Bolivia, *Antepirrhoe*
"*Perizoma*" *vacillans tolimensis* Prout, 1922 (type image checked)	unknown, Colombia, *Perizoma*
"*Perizoma*" *venisticta* (Dognin, 1912) (type image checked)	probably Plemyriopsini, *Alydda*; Colombia, *Psaliodes*
"*Perizoma*" *versatilis* Dognin, 1911 (type image checked)	Plemyriopsini, *amplata*-group; Colombia, *Perizoma*
"*Perizoma*" *vireonaria* (Maassen, 1890) (analysed)	Plemyriopsini, Ecuador, *Cidaria*
"*Perizoma*" *virescentaria* (Maassen, 1890) (not analysed)	unknown, Bolivia, *Thalassodes*
"*Psaliodes*" *picta* Warren, 1904 (analysed)	Plemyriopsini, Peru, *Psaliodes*
"*Larentia*" *irma* Prout, 1923 (analysed)	unknown, Argentina, *Larentia*
"*Larentia*" *macerata* (Felder & Rogenhofer, 1875) (analysed)	Ennadini, Chile, *Heterusia?*
"*Larentia*" *albifilata* Walker, [1863] (not analysed)	unknown, Venezuela, *Larentia*
"*Larentia*" *baliata* Herrich-Schäffer, 1870 (not analysed)	unknown, Cuba, *Larentia*
"*Larentia*" *danae* (Druce, 1893) (type image checked)	unknown, Mexico, *Eubolia*
"*Larentia*" *horismeata* Fletcher, 1953 (type image checked)	unknown, Argentina, *Larentia*
"*Larentia*" *lineolaria* Blanchard, 1852 (not analysed)	unknown, Chile, *Larentia*
"*Larentia*" *omphacina* Dognin, 1901 (not analysed)	likely Ennadini, Brazil, *Larentia*
"*Larentia*" *scarata* (Felder & Rogenhofer, 1875) (type image checked)	likely Ennadini, Chile, *Fidonia*
"*Larentia*" *subgaliata* Herrich-Schäffer, 1870 (not analysed)	unknown, Cuba, *Larentia*
"*Scopteryx*" *ferridotata* Walker, [1863]* (analysed)	Larentiini, South Africa, *Eubolia*
"*Stamnodes*" *eludens* (Warren, 1908) (type image checked)	Stamnodini, Peru, *Marmopteryx*
"*Stamnodes*" *instar instar* (Dognin, 1904) (type image checked)	Stamnodini, Peru, *Cophocerotis*
"*Stamnodes*" *instar casta* (Dognin, 1904) (not analysed)	Stamnodini, Peru, *Cophocerotis*
"*Stamnodes*" *uniformata* (Warren, 1877) (type image checked)	Stamnodini, Argentina, *Carisa*
"*Stamnodes*" *unilineata* (Walker, 1867) (not analysed)	unknown, Colombia, *Tora*

most lineage of Cidariini, although with poor support. A formal description will be given by Õunap et al. (in prep).

4.2.17. Cidariini. The Nearctic taxa *Ceratodalia gueneata* Packard, 1876 and *Trichodezia albovittata* Guenée, [1858] clearly belong to this clade. Both are type species of their genera, respectively. We transfer *Ceratodalia* Packard, 1876 from Hydriomenini to Cidariini (Table 1). *Trichodezia* Warren, 1895 was assigned to Cidariini by Viidalepp (1996, 2011) already. Our results support this view but not the assignment to Asthenini by Ferguson (1983) and Pohl et al. (2015, 2018).

4.2.18. Scotopterygini. We are not aware of any New World members of this tribe. We transfer the South African taxon *bitrita* Felder & Rogenhofer, 1875 from *Larentia* Treitschke, 1825 to *Scotopteryx* Hübner, [1825], and the South African taxon *epipercna* Wehrli, 1931 from *Perizoma* to *Scotopteryx* (Table 1).

4.2.19. Euphyiini-Xanthorhoini complex. The following six clades form a well supported lineage, and we considered other systematic options, i.e. either the fusion into a single large tribe Euphyiini, or a split into Euphyiini + unnamed clade + Xanthorhoini as well. We opted for a solution of five named clades and one unnamed clade, as Cataclysmini are a clearly distinct group according to the morphology of both male and female genitalia (for details see Hausmann & Viidalepp 2012).

4.2.19.1. Unnamed clade. The node supporting this clade as sister to Euphyiini is not strongly supported (SH-like = 28.1, UFBoot2 = 71). Its phylogenetic position and taxonomic rank thus requires further study. The clade comprises *Disclisioprocta* Wallengren, 1861 (assigned to Xanthorhoini by Pohl et al. 2018) and unassigned *Ptychorrhoe* Warren, 1900. Morphology (e.g. genitalia) of the widespread New World species *D. stellata* (Guenée, [1858]) clearly shows that it is congeneric with the two valid Old World taxa (our sample is *D. natalata* Walker, 1862) (A.H., unpublished data). It seems, however, uncertain whether the type species of *Ptychorrhoe*, *P. rayada* Dognin, 1893, is actually congeneric with *P. blosyrata* (Guenée, [1858]) because the wing pattern of these two species differ substantially (see photos in Electronic Supplement File 4).

4.2.19.2. Euphyiini. Results show that *Euphyia* Hübner, [1825] is present both in the Neotropical region and in the Holarctic region. We transfer the species *tricolorata* Dognin, 1902 from *Xanthorhoe* Hübner, [1825] to *Euphyia* (Table 1). Our analysis also includes *Oligopleura* Herrich-Schäffer, [1855] (Fig. 3I) and *Hammaptera* Herrich-Schäffer, [1855], the latter for the first time in a molecular phylogenetic analysis.

4.2.19.3. Pterocyphini Brehm, Murillo-Ramos & Õunap, new tribe. — **Type genus.** *Pterocypha* Herrich-Schäffer, [1855] (Fig. 3J). — **Material examined and phylogeny.** This clade comprises *Pterocypha*, *Obila* Walker, 1869, and *Archirhoe* Herbulot, 1951. Our current knowledge suggests that Pterocyphini are possibly restricted to the New World. We analysed the type species of *Pterocypha*, *gibbosaria* Herrich-Schäffer, [1855]. Branch support values from the IQ-TREE analyses clearly confirm the monophyly of this clade (SH-like = 100, UFBoot2 = 99). — **Molecular evidence.** The tribe is characterized by DNA sequence data from the following seven gene regions (exemplar *P. gibbosaria*, voucher Br-Geo-0059 from Brazil, illustrated in Electronic Supplement File 5): ArgK (MK738221), Ca-ATPase (MK738618), COI (MK739110), EF1a (MK739723), Nex9 (MK741384), RPS5 (MK741726). Wingless (MK742188). — **Morphology.** External features of analysed species are illustrated in Fig. 3J and Electronic Supplement File 4. Further detailed morphological analysis is required to identify potential diagnostic features. — **Remarks and taxonomic changes.** We transfer *Archirhoe* from Hydriomenini and *Obila* and *Pterocypha* from unassigned to Pterocyphini (Table 1).

4.2.19.4. Xanthorhoini. Our analysis include *Helastia* Guenée, 1868, *Orthonama* Hübner, [1825] (Fig. 3K), and *Xanthorhoe* Hübner, [1825], the latter genus including representatives from both the New and the Old World. Judged by wing morphology, we transfer the taxon *inflexa* Dognin, 1914 from *Scotopteryx* to *Orthonama* (illustrated in Electronic Supplement File 4, Table 1).

4.2.19.5. Cataclysmini. Our analysis includes *Cataclysme* Hübner, [1825], *Phibalapteryx* Stephens, 1829, and *Zenophleps* Hulst, 1896, the latter being transferred to Cataclysmini from Xanthorhoini (Table 1). *Zenophleps* is an exclusively Nearctic genus.

4.2.19.6. Epirrhoini, stat.rev. We revive Pierce's (1914) Epirrhoinae (which comprised both *Epirrhoe* Hübner, [1825] and *Catarhoe* Herbulot, 1951 in his treatment) at the tribe level as Epirrhoini. Since "*Euphyia*" *sturnularia* Herrich-Schäffer, [1855] is misplaced, the genus should be listed – ad interim – with quotation marks (illustrated in Fig. 3L). Herewith, we include *sturnularia* in Epirrhoini as well as the African *Mimoclystia* Warren, 1901 (Table 1). Further study must reveal the relationship between Neotropical *sturnularia* and the Old World genera *Catarhoe*, *Mimoclystia* and *Epirrhoe* Hübner, [1825].

4.2.20. Larentiini complex. All following Larentiinae taxa form a large, rather well supported clade (SH-like = 87, UFBoot2 = 79) with a dominance of Neotropical taxa. Palaearctic species are represented in our dataset with one or a few species in Larentiini, Ennadini, Hydriomenini and Stamnodini – but more sampling in the Old World is required. Genetic divergences between the lineages proposed as tribes Heterusiini, Cophocerotini, Erateinini, Erebochlorini and Stamnodini are rather small, and all these tribes could potentially be synonymized with Hydriomenini. However, many of the currently recognized tribes are rather species-rich (Hydriomenini, Heterusiini, Erateinini, Stamnodini), and there is considerable diversity in the external morphology of the moths (Fig. 3M – T), possibly related to several switches to diurnal lifestyle (in particular the genera *Hagnagora*, *Heterusia* Hübner, [1825] and *Erateina* Doubleday, 1848), see Brehm & Sullivan (2005).

4.2.20.1. Rhinurini Brehm, Murillo-Ramos & Õunap, new tribe. — **Type genus.** *Rhinura* Warren, 1904 (Fig. 3M). — **Material examined and phylogeny.** *Rhinura* near *populonia* (Druce, 1893) is sister to *Haplolabida inaequata* (Prout, 1935). Rhinurini are sister to a large assemblage including e.g. Larentiini and Stamnodini (Fig. 2). Branch support values from the IQ-TREE analyses strongly confirm the monophyly of this clade (SH-like = 99.9, UFBoot2 = 100). — **Molecular evidence.** The tribe is characterized by DNA sequence data from the following seven gene regions (exemplar *Rhinura* near *populonia*, voucher EO1166 from Ecuador, illustrated in Electronic Supplement File 5): CAD (MK738977), COI (MK739207), EF1a (MK739789), GAPDH (MK740423), IDH (MK740793), RPS5 (MK741786), Wingless (MK742294). — **Morphology.** External features of analysed species are illustrated in Fig. 3M and Electronic Supplement File 4. Further detailed morphological analysis is required to identify potential diagnostic features. — **Remarks and taxonomic changes.** This tribe currently comprises only two genera from different continents. More taxon sampling is required to show whether more African genera might belong to Rhinurini. We also transfer the monotypic Neotropical genus *Urocalpe* Warren, 1904 to Rhinurini, based on the wing pattern that is very similar to that of *Rhinura* (illustrated in Electronic Supplement File 4, Table 1). Comprehensive further morphological and molecular study is required.

4.2.20.2. Larentiini. Our analysis comprises no species from the New World in this tribe. Since the following species are misplaced, the respective genus should be listed – ad interim – with quotation marks: Old World "*Perizoma*" *alumna* (Prout, 1925) (see Perizomini) and "*Scotopteryx*" *ferridotata* (Walker, [1863]) (see Scotopterygini) (Table 1). An integrative revision of the aforementioned taxa is required to provide new nomenclatorial combinations.

4.2.20.3. Unnamed clade. This clade comprises four species: One is unidentified, one is "*Larentia*" near *irma*

Prout, 1923 from Chile (illustrated in Electronic Supplement File 4), and two are wrongly assigned to *Heterusia* Hübner, [1825]. Since "*Heterusia*" *picata* Dognin, 1904 and "*Heterusia*" *plagia* Druce, 1893 are misplaced, the genus should be listed – ad interim – with quotation marks (illustrated in Electronic Supplement File 5, Table 1). Since *Heterusia* comprises more species with *plagia*-like habitus (e.g. *polymela* Druce, 1893 and *prusa* Druce, 1893) it is likely to be non-monophyletic and requires revision. A formal description of a new tribe is not performed because the taxonomy of the examined material is still unclear.

4.2.20.4. Ennadini Brehm, Murillo-Ramos & Õunap, new tribe. — **Type genus.** *Ennada* Blanchard, 1852 (Fig. 3N). — **Material examined and phylogeny.** The clade comprises mostly species misplaced in the genera *Hagnagora*, *Larentia*, *Perizoma*, and *Nebula*. It also comprises *Ennada* and three species of *Spargania* Guenée, [1858], a genus previously assigned to Larentiini (Hausmann & Viidalepp 2012). The type species of the genus, *S. magnoliata* Guenée [1858] from North America, is not included in the analysis. However, *S. magnoliata* and Palaearctic *S. luctuata* ([Denis & Schiffermüller], 1775) are actually congeners (E.Õ. and Andro Truuverk, unpublished). Branch support values from the IQ-TREE analyses confirm the monophyly of this clade (SH-like = 97.5, UFBoot2 = 71). — **Molecular evidence.** The tribe is characterized by DNA sequence data from the following five gene regions (exemplar *Ennada pellicata* Felder & Rogenhofer, 1875, voucher Ch-Geo-0010 from Chile, illustrated in Electronic Supplement File 5): COI (MK739121), EF1a (MK739731), MDH (MK740958), RPS5 (MK741737), Wingless (MK742200). — **Morphology.** External features of all analysed species are illustrated in Fig. 3N and Electronic Supplement File 4. Further detailed morphological analysis is required to identify potential diagnostic features. — **Remarks and taxonomic changes.** *Ennada* species were revised by Parra & Alvear (2009). All Chilean species of the genera *Hagnagora*, *Larentia* and *Nebula* are misplaced to the respective genera, which therefore should be listed – ad interim – with quotation marks (Table 1). "*Hagnagora*" *mesenata* Felder & Rogenhofer, 1875 was already proposed to be excluded from *Hagnagora* by Brehm (2015). An integrative revision of the mentioned taxa is required to provide new nomenclatorial combinations. We formally transfer the taxa *coeruleopicta* Warren, 1908 and *emmelesiata* Snellen, 1874 to *Spargania* because they are apparently closely related to *S. zenobia* (Table 1).

4.2.20.5. Hydriomenini. This lineage includes five analysed taxa, among them two European and one Neotropical species of *Hydriomena* Hübner, [1825]. Monotypic *Cyclica* Grote, 1882, is nested within *Hydriomena* and is therefore synonymized (Table 1). *Ersephila prema* Druce, 1893 (Fig. 3O) is sister to the other four analysed species. *Ersephila* Hulst, 1896 is retained but it remains to be shown in further studies whether *Ersephila* is monophyletic.

4.2.20.6. Heterusiini. The clade includes the Neotropical genera *Heterusia* Hübner, [1831] and *Spiloctenia* Warren, 1897, both represented by their type species in the analysis (Fig. 3P: *H. quadruplicaria* Geyer, 1832). *Spiloctenia* is transferred from unassigned to Heterusiini which is plausible also from wing morphology (illustrated in Electronic Supplement File 4, Table 1).

4.2.20.7. Cophocerotini Brehm, Murillo-Ramos & Õunap, new tribe. — **Type genus.** *Cophocerotis* Warren, 1895 (Fig. 3Q). — **Material examined and phylogeny.** The clade includes *Cophocerotis* and *Hagnagora*. We chose *Cophocerotis* for naming the tribe because there are morphological differences between the analysed *Hagnagora* species and the type species *H. buckleyi* Druce, 1885 (Brehm 2015), questioning their status as congeners. Branch support values from the IQ-TREE analyses confirm the monophyly of Cophocerotini (SH-like = 100, UFBoot2 = 100). — **Molecular evidence.** The tribe is characterized by DNA sequence data from the following seven gene regions (exemplar *Cophocerotis costinotata* Warren, 1908, voucher gb-ID-19302 from Ecuador, illustrated in Electronic Supplement File 5): COI (MK739304), EF1a (MK739882), GADPH (MK740547), MDH (MK741090), Nex9 (MK741533), RpS5 (MK741896), Wingless (MK742433). — **Morphology.** External features of analysed species are illustrated in Fig. 3Q and Electronic Supplement File 4. Further detailed morphological analysis is required to identify potential diagnostic features. — **Remarks and taxonomic changes.** The analysis of the phylogenetic placement of *Hagnagora buckleyi* urgently requires to be studied. If it turns out not to be congeneric with other species currently assigned to *Hagnagora*, those will need to be transferred to another genus.

4.2.20.8. Erateinini. The clade includes the genera *Erateina* Doubleday, 1848 (Fig. 3R) and *Anemplocia* Warren, 1905. It also includes the taxon "*Trocherateina*" Prout, but according to Scoble (1999), this name had not been published before. As the most straight-forward way towards a system of monophyla, we synomynize *Anemplocia*, and transfer all species currently assigned to unavailable "*Trocherateina*" to *Erateina* (Table 1).

4.2.20.9. Erebochlorini Brehm, Murillo-Ramos & Õunap, new tribe. — **Type genus.** *Erebochlora* Warren, 1895 (Fig. 3S). — **Material examined and phylogeny.** This clade includes the three Neotropical genera *Erebochlora*, *Cirrolygris* Warren, 1895, and *Deinoptila* Warren, 1900. Branch support values from the IQ-TREE analyses clearly support the monophyly of this clade (SH-like = 100, UFBoot2 = 100). — **Molecular evidence.** The tribe is characterized by DNA sequence data from the following eight gene regions (exemplar *Erebochlora* near *tesserulata* Felder & Rogenhofer, 1875, voucher GB-CR-1218, from Costa Rica, illustrated in Electronic Supplement File 5): ArgK (MK738311), Ca-ATPase (MK738705), COI (MK739228), EF1a (MK739809), GAPDH (MK740443), MDH (MK741007), Nex9

(MK741444), Wingless (MK742314). — **Morphology.** External features of all analysed species are illustrated in Fig. 3S and Electronic Supplement File 4. Further detailed morphological analysis is required to identify potential diagnostic features. — **Remarks and taxonomic changes.** *Priapodes* Warren, 1895 was described by Warren only because of prolonged palpi; he stated that "otherwise the types of the two genera [*Priapodes* and *Erebochlora*] are superficially wonderfully alike". Since the two genera indeed have a very similar habitus, size and wing pattern (illustrations in Electronic Supplement File 5), we synonymize *Priapodes* with *Erebochlora* (Table 1). We suggest to place the genus of "*Erebochlora*" *apiciflava* Dognin, 1892 – ad interim – in quotation marks, as it was recovered apart form its congeners and sister to a clade comprising *Cirrolygris* and *Deinoptila* (Table 1). Further study of *Erebochlora* is required because it currently is a paraphyletic assemblage.

4.2.20.10. Stamnodini. Our analysis includes the Palaearctic type species of *Stamnodes* Guenée, [1858], viz. *S. pauperaria* Eversmann, 1848 and the Nearctic *S. topazata* Strecker, 1899 (Õunap et al. 2016). We also analysed the taxon *triangularia* Bartlett-Calvert, 1891. As a step towards a natural system, we revive *Synneuria* Mabille, 1885, from synonymy with *Stamnodes* and transfer three more species that were originally described in *Synneuria* back to this genus (Table 1). The Neotropical species *anthocharidaria* Oberthür, 1881 (Fig. 3T) is sister to *Callipia* Guenée, [1858]. We therefore transfer it from *Stamnodes* to *Callipia* (Table 1). *C. anthocharidaria* has a similar general habitus and wing shape as *Callipia* species (Brehm 2018), although its wing pattern is largely reduced and it is considerably smaller than all previously known *Callipia* species (illustrations in Electronic Supplement File 4). Four South American "*Stamnodes*" species are misplaced, and their genus name should be listed – ad interim – with quotation marks. Moreover, we transfer the genera *Pseudopsodos* Thierry-Mieg, 1903, and *Scordyliodes* Thierry-Mieg, 1903 to Stamnodini (Table 1).

4.3. Archiearinae Fletcher, 1953

Archiearinae are represented, in our analysis, by four species, including two Nearctic taxa. Nearctic *Archiearis infans* Möschler, 1862 clusters together with Palaearctic *A. parthenias* (Linnaeus, 1761) while *Leucobrephos brephoides* (Walker, 1857) is sister to *Archiearis* Hübner, [1823] + *Boudinotiana* Hübner, [1803] clade. The sister relationship of *Leucobrephos* Grote, 1874 with *Archiearis* + *Boudinotiana* is plausible and well confirmed by morphology (Müller et al. 2019). The Australian genera *Dirce* Prout, 1910 and *Acalyphes* Turner, 1926 were transferred from Archiearinae to Ennominae earlier (Young 2006; Murillo-Ramos et al. 2019). Representatives from Central and South America await further study, i.e. *Caenosynteles* Dyar, 1912 (one species), *Archiearides* Fletcher, 1953 (two species), and *Lachnocephala* Fletcher, 1953 (one species). There is evidence that at least *Archiearides* indeed belongs to Archiearinae because of a "Archiearinae-like" tympanum (Fletcher 1953; Cook & Scoble 1992). On the other hand, the very isolated distribution of the austral South American taxa suggests possible convergence with Holarctic taxa due to similar (diurnal) behaviour and resulting similar colour patterns (illustrations in Electronic Supplement File 4).

4.4. Desmobathrinae Meyrick, 1886, Oenochrominae Guenée, [1858], Epidesmiinae Murillo-Ramos, Sihvonen & Brehm, 2019

These subfamilies were treated in detail by Murillo-Ramos et al. (2019). Six Neotropical genera in two separate lineages belong to the Desmobathrinae: *Zanclopteryx* Herrich-Schäffer, [1855] clusters together with *Ozola* Walker, 1861. The second clade comprises Neotropical *Racasta* Walker, 1861, *Leptoctenopsis* Warren, 1895, *Ophiogramma* Hübner, [1831], *Pycnoneura* Warren, 1894 and *Dolichoneura* Warren, 1894 as sister to the Indopacific genus *Noreia* Walker, 1861. There are no representatives of the subfamilies Oenochrominae, Epidesmiinae and Orthostixinae from the New World in our analysis. We could not study two monotypic New World genera currently assigned to Oenochrominae, viz. *Carmala* Walker, [1863] and *Cortixa* Schaus, 1901. *Carmala* is unknown to us, and *Cortixa* comprises small and slender-bodied moths that are more likely to belong to Desmobathrinae than to Oenochrominae.

4.5. Geometrinae Stephens, 1829

See Fig. 4 for phylogenetic relationships, Fig. 5 for habitus pictures of exemplary species, and Table 2 for proposed taxonomic changes.

By far most sampled New World Geometrinae taxa are concentrated in the New World tribe Nemoriini, a group recently studied in detail by Viidalepp (2017). Apart from *Nemoria* Hübner, with its type species *bistriaria* Hübner, 1818 (Fig. 5A), our data confirm the assignment to Nemoriini of the genera *Assachlora* Viidalepp & Lindt, 2012, *Chavariella* Pitkin, 1993, *Dichorda* Warren, 1900, *Hyalochlora* Prout, 1912, *Lissochlora* Warren, 1900, *Neagathia* Warren, 1897, *Phrudocentra* Warren, 1895, *Pyrochlora* Warren, 1895, *Rhodochlora* Warren, 1894, *Tachyphyle* Butler, 1881 and *Tachychlora* Prout, 1912. In addition, our data suggest that the currently unassigned genus *Hydata* Walker [1863] also needs to be transferred to Nemoriini: (Table 2). Viidalepp (2017) discussed the absence of a midrib of the last abdominal sternite of the male as a basic nemoriine characteristic of *Hydata* and *Methydata* Prout, 1933, but he also found possible other synapomorphies linking them with Nemoriini.

The Synchlorini genus *Synchlora* Guenée, [1858] – represented with its type species *aerata* (Fabricius, 1798)

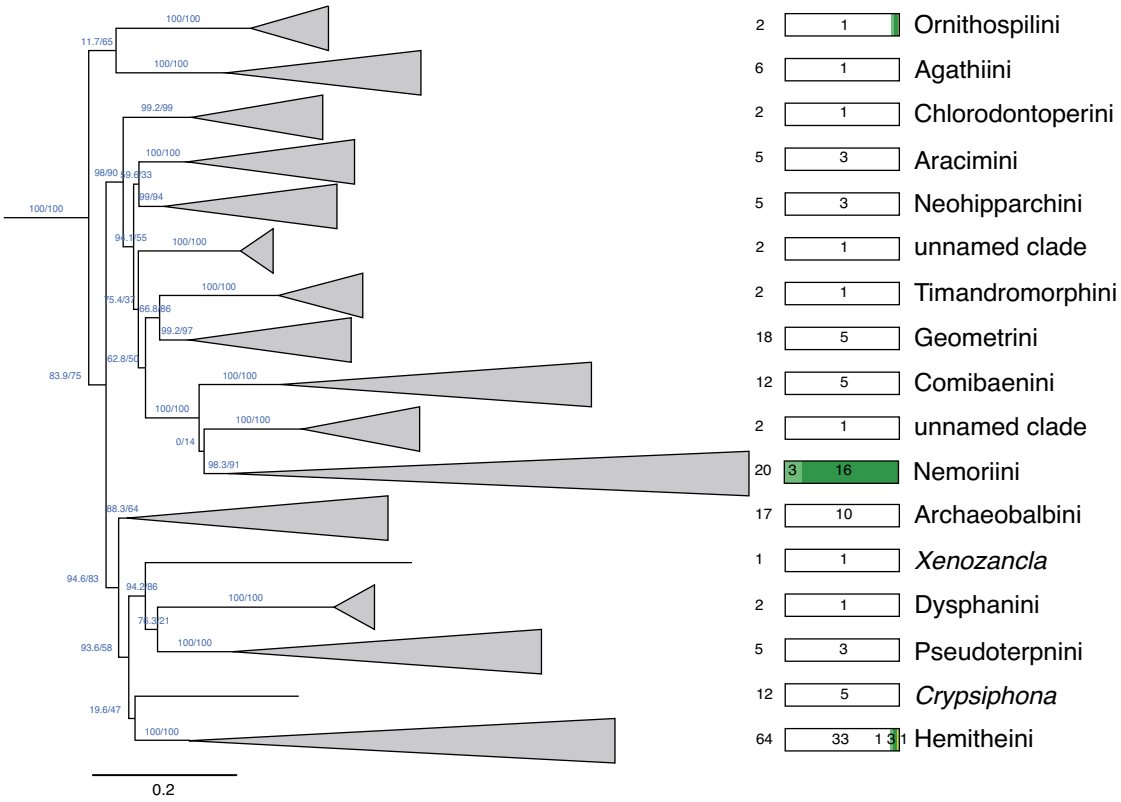

Fig. 4. Geometrinae tribe composition. Tribes with New World representatives marked in colour: light green Nearctic, dark green Neotropical, yellowish green austral region; see also explanatory box in Fig. 1. Support values in blue colour (SH-like and UFBoot values).

(Fig. 5B) – is nested within Nemoriini. Murillo-Ramos et al. (2019) therefore synonymized Synchlorini with Nemoriini. Our data show that *Nemoria* itself is not monophyletic and requires revision which, however, is beyond the scope of our study. Possible steps towards a system of natural entities could include the transfer of (presumably many) species around *N. nigrisquama* (Dognin, 1904) (Fig. 5C) to *Lissochlora* (Fig. 5D) and reviving one or more generic synonyms of *Nemoria* in future studies. In our study, we recognize the studied species *nigrisquama* and *erina* (Dognin, 1896) (Fig. 5E) as misplaced in *Nemoria*. For these cases, we suggest that the genus is listed – ad interim – with quotation marks (Table 2). An integrative revision of the mentioned taxa is required to provide new nomenclatorial combinations.

Only a few studied New World Geometrinae taxa belong to tribes other than Nemoriini. In the Hemitheini, *Lophochorista* Warren, 1904 (Fig. 5F) defines the Lophochoristina (Lophochoristini in Pitkin 1996, Lophochoristiti in Ban et al. 2018), but its closest relatives are the unassigned African genera *Rhadinomphax* Prout, 1912 and *Adicocrita* Prout, 1930 which we formally assign to the subtribe Lophochoristina (Table 2). Two other New World genera form a monophylum: *Anomphax* Warren, 1909 (Fig. 5G) and *Oospila* Warren, 1897. They are not closely related to *Lophochorista*, and therefore are not part of Lophochoristina (Table 2). The position of *Chloropteryx* Hulst, 1896 (Fig. 5H) and *Xerochlora* Ferguson, 1969 in Hemitheini/Hemitheina confirms previous results (Pitkin 1996). The North American genus *Dichordophora* Prout, 1913 needs to be investigated in future studies because it is representing the tribe Dichordophorini (Ferguson 1969).

4.6. Ennominae Duponchel, 1845

See Fig. 6 for phylogenetic relationships, Fig. 7 for habitus pictures of exemplary species, and Table 3 for proposed taxonomic changes.

Species from the New World are present in the large majority of Ennominae tribes (Fig. 6), and the subfamily is doubtlessly the most species-rich subfamily in this region (Piktin 2002). In addition to Palyadini and probably Nacophorini, three new tribes (see below: Euangeronini, Oenoptilini, Pyriniini) comprise exclusively Neotropical genera. It remains to be shown whether further taxon sampling in the Old World and Australasia will add taxa from these regions.

4.6.1. Euangeronini Brehm, Murillo-Ramos & Sihvonen, new tribe. — **Type genus.** *Euangerona* Butler, 1882 (Fig. 7A). — **Material examined and phylogeny.** The tribe exclusively comprises taxa from austral South America and is related to a clade comprising only *Idialcis* Warren, 1906, Gonodontini and Gnophini. None of those are morphologically similar to Euangeronini (see illustrations in Pitkin 2002 and Müller et al. 2019). Further analysed genera included in the tribe: *Dectochilus* Butler, 1882, *Malleco* Rindge, 1971, and *Odontothera*

Table 2. Taxonomic changes in Geometrinae at the level of tribes, genera and species, in alphabetical order. *Old World taxa.

From tribe *x* to tribe *y*	**Genus**
unassigned to Nemoriini	*Hydata* Walker, 1895
Genus	**From subtribe *x* to subtribe *y***
Rhadinomphax Prout, 1912*	unassigned to Lophochoristina
Adicocrita Prout, 1930*	unassigned to Lophochoristina
Anomphax Warren, 1909	Lophochoristina to unassigned
Oospila Warren, 1897	Lophochoristina to unassigned
Species proposed to be excluded from genera = *incertae sedis*	**Tribe assignment, country, originally described in genus**
"Nemoria" nigrisquama Dognin, 1904	Nemoriini, Peru, *Miantonota*
"Nemoria" erina Dognin, 1896	Nemoriini, Ecuador, *Achlora*

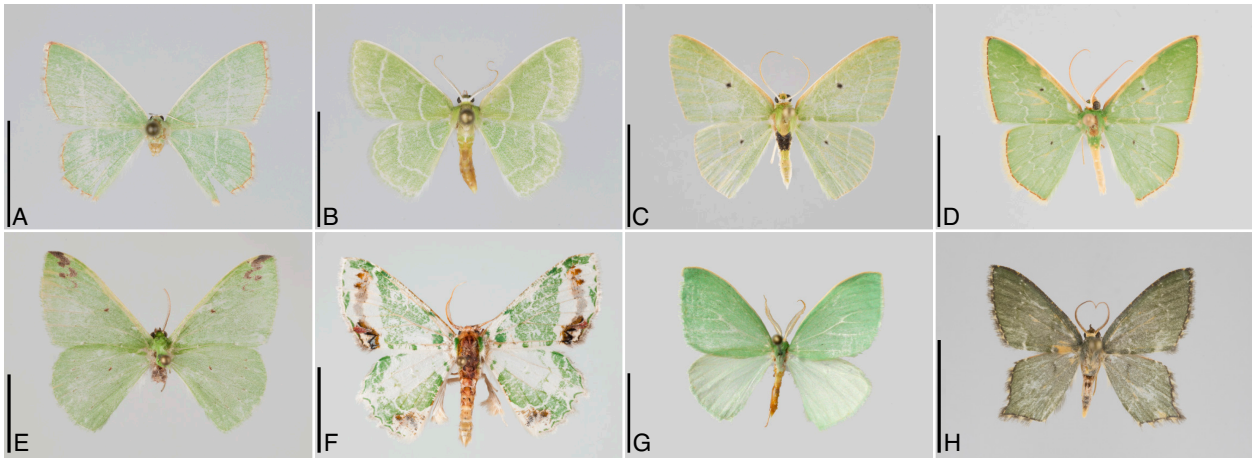

Fig. 5. Illustrations of selected Neotropical Geometrinae taxa. **A**: Nemoriini, *Nemoria bistriaria* Hübner, 1818 (CNC580945). **B**: Nemoriini, *Synchlora aerata* (Fabricius, 1798) (CNC541241). **C**: Nemoriini, "*Nemoria*" *nigrisquama* (Dognin, 1904) (Pe-Geo-3142) **D**: Nemoriini, *Lissochlora latuta* (Dognin, 1898) (ID 18194). **E**: Nemoriini, "*Nemoria*" *erina* (Dognin, 1896) (AH7057). **F**: Hemitheini, *Lophochorista* near *curtifascia* Prout, 1933 (GB-Geo-083). **G**: Hemitheini, *Anomphax gnoma* (bo_chi_433). **H**: Hemitheini, *Chloropteryx* sp. (Pe-Geo-0614).

Butler, 1882. We also examined "*Opisogonia*" *diffissata* Felder & Rogenhofer, 1875 and "*Chlorochlydon*" *rinodaria* Felder & Rogenhofer, 1875. Both are not congeneric with the type species of the respective genera (Pitkin 2002), see photos in Electronic Supplement File 1. *Chloroclydon* Warren, 1894, is a junior synonym of *Herochroma* Swinhoe, 1893, an Old World Geometrinae genus. Branch support values from the IQ-TREE analyses clearly confirm the monophyly of Euangeronini (SH-like = 99.5, UFBoot2 = 96). — **Molecular evidence.** The tribe is characterized by DNA sequence data from the following five gene regions (exemplar *Euangerona valdiviae* Butler, 1882, voucher bo-chi-109 from Chile, illustrated in Fig. 7A): Ca-ATPase (MK738586), COI (MK739063), EF1a (MK739698), Nex9 (MK741345), RPS5 (MK741700). — **Morphology.** External features of analysed species are illustrated in Fig. 7A and Electronic Supplement File 5. Further detailed morphological analysis is required to identify potential diagnostic features. — **Remarks and taxonomic changes.** We provisionally also assign *Omaguacua* Rindge, 1983 to Euangeronini because it is similar to *Dectochilus* according to its external morphology, however without dentate forewing margins (illustrated in Electronic Supplement File 5). See Pitkin (2002) for more information on the included genera and species.

4.6.2. Unnamed clade. *Idialcis* Warren, 1906 (Fig. 7B), is part of the Euangeronini-Gonodontini-Gnophini clade. It is an independent lineage which might represent a separate tribe and requires further study. *Idialcis* is transferred from Ennomini to unassigned (Table 3).

4.6.3. Gonodontini. This tribe is represented by two Old World genera in our phylogeny and it is unlikely that Gonodontini are represented in the New World. The type genus of the tribe, *Gonodontis* Hübner, [1823], was not included in the analysis.

4.6.4. Gnophini. This tribe comprises only a few New World taxa in our analysis, namely Nearctic *Euchlaena* Hübner, [1823], and *Lytrosis* Hulst, 1896. These were assigned to Angeronini by Ferguson (1983) but we follow recent literature (e.g. Skou & Sihvonen 2015; Beljaev 2016; Müller et al. 2019; Murillo Ramos et al. 2019) who considered Angeronini a junior synonym of Gnophini. The Chilean genus *Neorumia* Bartlett-Calvert, 1893 (see Parra & Vargas 2000) can be assigned to

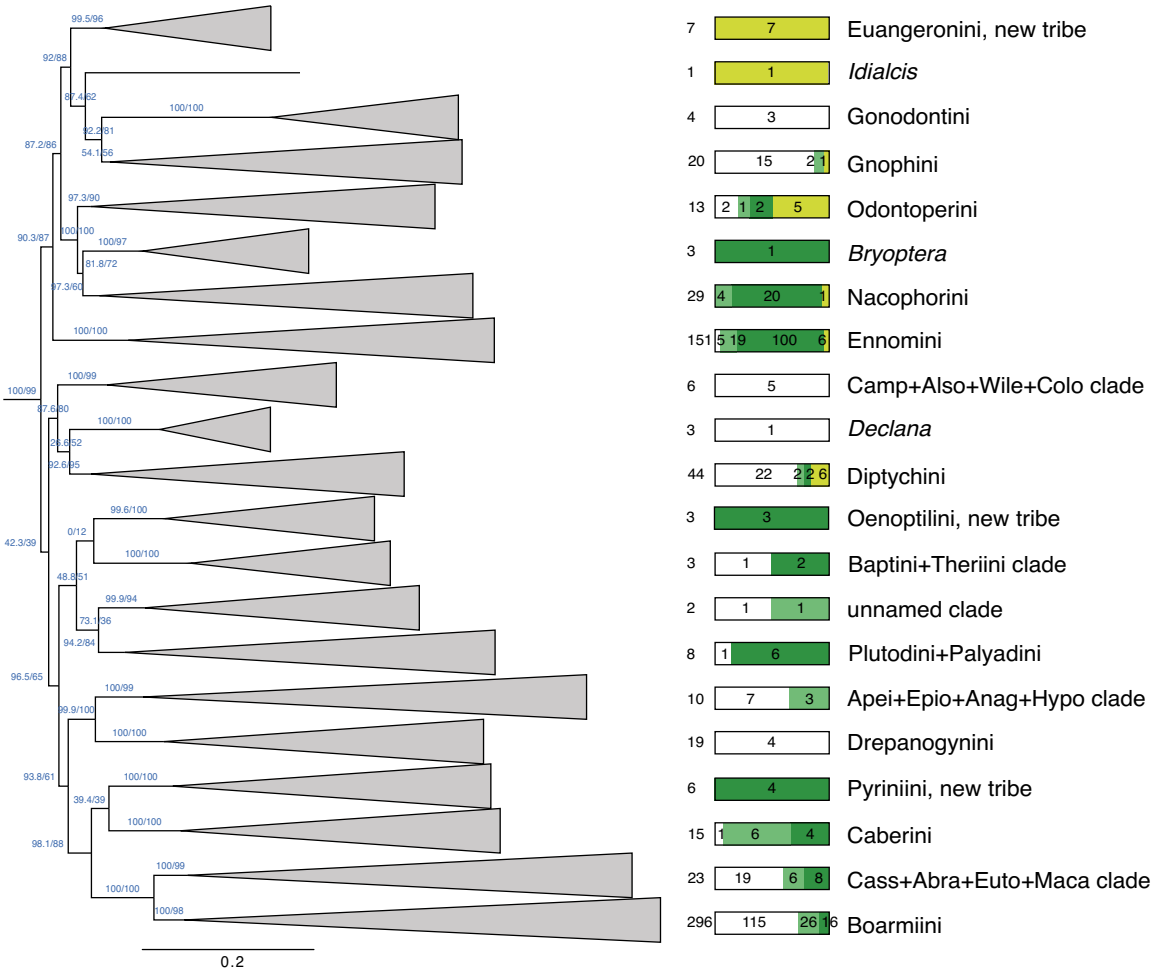

Fig. 6. Ennominae tribe composition. Tribes with New World representatives marked in colour: light green Nearctic, dark green Neotropical, yellowish green austral region; see also explanatory box in Fig. 1. Camp+Also+Wile+Colo: Campaeini + Alsophilini + Wilemaniini + Prosopolophini clade. Ther+Bapt+Plut+Paly: Theriini + Baptini + Plutodini + Palyadini clade. Apei+Epio+Anag+Hypo: Apeirini + Epionini + Anagogini + Hypochrosini clade. Cass+Abra+Euto+Maca: Cassymini + Abraxini + Eutoeini + Macariini clade. Support values in blue colour (SH-like and UFBoot values).

Gnophini (Fig. 7C, Table 3). However, "*Neorumia*" *gracilis* Bartlett-Calvert, 1893 was already excluded from *Neorumia* by Pitkin (2002) and clusters in Ennomini.

4.6.5. Odontoperini. This clade comprises the type species of *Odontopera* Stephens, 1831, Palaearctic *O. bidentata* Clerck, 1759, *Henicovalva* Krüger, 2017 from South Africa, *Nemeris* Rindge, 1981 from North America and the austral South American genera *Dentinalia* Heimlich, 1960, *Macrolyrcea* Butler, 1882, *Mallomus* Blanchard, 1852, *Praeantarctia* Heimlich, 1956, and *Talca* Rindge, 1971. All these genera (except for *Odontopera*) are transferred to Odontoperini (Table 3). The Azelinini are nested within Odontoperini and are therefore synonymized with it (Table 3). Members of the tribe Odontoperini have recently been classified as Ennomini of uncertain association (Skou & Sihvonen 2015) or as Odontoperini (Beljaev 2016). *Nepitia* Walker, 1866, is nested within *Pero* Herrich-Schäffer, 1855, and is therefore synonymized with it (Fig. 7D, Table 3). A close relationship of Odontoperini, Azelinini and Nacophorini was already suggested by Holloway (1994), with a possible synapomorphy of 16 setae on the proleg of the caterpillar on A6, and our data provide strong support for this hypothesis.

4.6.6. Unnamed clade. *Bryoptera* Guenée, [1858] forms a lineage of its own that cannot clearly be assigned to either Odontoperini or Nacophorini. *Bryoptera* has previously been assigned to Boarmiini because of its Boarmiini-like wing pattern (illustrated in Electronic Supplement File 5), but Pitkin (2002) already noted that its genitalia characters were unusual for that tribe. *Bryoptera* is transferred from Boarmiini to unassigned (Table 3), but it is certainly part of the Odontoperini-Nacophorini clade. *Tephrosia vaga* Dognin, 1895 is transferred from "*Ectropis*" to *Bryoptera* (Fig. 7E, Table 3). Three Chilean species previously assigned to *Bryoptera* were transferred to *Leucolithodes* by Parra & Hormazábal (1993).

4.6.7. Nacophorini. Many species from all around the world have been assigned to this tribe, but our results clearly show that Nacophorini are a New World clade, as previously stated by Young (2003). *Nacophora* Hulst, 1896 is a junior synonym of *Phaeoura* Hulst, 1896. The

Fig. 7. Illustrations of selected Neotropical Ennominae taxa. **A**: Euangeronini, **new tribe**, *Euangerona valdiviae* Butler, 1882 (bo_chi_109). **B**: unnamed clade, *Idialcis jacintha* (Butler, 1882) (bo_chi_648). **C**: Gnophini, *Neorumia gigantea* Bartlett-Calvert, 1893 (bo_chi_167). **D**: Odontoperini, *Pero detractaria* (Walker, 1866) **comb.n.** (Pe-Geo-0659). **E**: unnamed clade, *Bryoptera vaga* (Dognin, 1895) **comb.n.** (gb-ID-22872). **F**: Nacophorini, *Phaeoura quernaria* (Smith, 1797) (CNC583542). **G**: Ennomini, "*Nephodia*" *panacea* Thierry-Mieg, 1892 (AH7126). **H**: Ennomini, "*Perusia*" *viridis* Warren, 1907 (Pe-Geo-0680). **I**: Prosopolophini, *Himeromima aulis* Druce, 1892 (Gu-Geo-005). **J**: Diptychini, "*Loxaspilates*" *torcida* Dognin, 1900 (ID 19263). **K**: Oenoptilini, **new tribe**, *Oenoptila mixtata* Guenée, [1858] (Br-Geo-0006). **L**: Palyadini, *Ophthalmoblysis cinerea* (Warren, 1909) (Vz-Geo-014). **M**: unassigned to tribe, *Sericosema juturnaria* Guenée, [1858] (CNC533584). **N**: Pyriniini, **new tribe**, *Pyrinia abditaria* (Warren, 1905) (gb-ID-16080). **O**: Caberini, *Aplogompha lafayi* (Dognin, 1899) (Pe-Geo-0545). **P**: unassigned to tribe, *Hypometalla scintillans* Warren, 1906 (Pe-Geo-0503). **Q**: Cassymini s.l., *Leuciris beneciliata* Prout, 1910 (Pe-Geo-0545). **R**: Macariini, *Macaria cardinea* (Druce, 1893) (gb-ID-17469). **S**: Boarmiini, *Perigramma famulata* (Felder & Rogenhofer, 1875) (Pe-Geo-3039). **T**: Boarmiini, "*Synnomos*" near *apistrigata* Warren, 1895 (Br-Geo-0008).

type species of *Nacophora* is *Phaeoura quernaria* Smith, 1797 (Fig. 7F), and it is represented in our analysis. Nacophorini s.str. form a well supported clade, including (in addition to *P. quernaria*) the genera *Aethaloida* McDunnough, 1920, *Betulodes* Thierry-Mieg, 1904, *Gabriola* Taylor, 1904, *Holochroa* Hulst, 1896, and *Thyrinteina* Möschler, 1890. We suggest a concept of Nacophorini s.l., which at the moment includes New World genera only, with several well supported clades. One clade comprises the Neotropical genera *Charca* Rindge, 1983, *Chrysomima* Warren, 1894, *Cundinamarca* Rindge, 1983, *Ischnopteris* Hübner, [1823], *Paradoxodes* Warren, 1904, *Quillaca* Rindge, 1983, *Rucana* Rindge, 1983, *Stegotheca* Warren, 1900, an unnamed genus, and the Nearctic *Ceratonyx* Guenée, [1858] – all already assigned to Nacophorini. Another mostly Neotropical clade comprises *Achagua* Rindge, 1983, *Cargolia* Schaus, 1901, *Cidariophanes* Warren, 1895, *Eustenophasma* Warren, 1897, *Leucochesias* Mabille, 1889, *Nazca* Rindge, 1983, *Oratha* Walker, 1863, and *Postazuayia* Rindge, 1986. *Eustenophasma* and *Leucochesias* are transferred from unassigned to Nacophorini (Table 3). The colourful genus *Catophoenissa* Warren, 1894 and probably also the similar unsampled genus *Catocalopsis* Rindge, 1971 – il-

lustrated in Electronic Supplement File 5 – does not have a stable position in the tree. Australian "Nacophorini" (see for instance Young 2006, 2008) are mostly nested in Diptychini (see 4.6.11. below), and most African "Nacophorini" also belong to Diptychini or group together in Drepanogynini (Murillo-Ramos et al. 2019).

4.6.8. Ennomini. Ennomini are sister to a lineage comprising all aforementioned Ennominae clades (Fig. 6). An Old World lineage comprises both *Ennomos* Treitschke, 1825, and *Ourapteryx* Leach, 1814 (known from previous analyses, e.g. Sihvonen et al. 2011). Both taxa are closely related and we therefore agree with the synonymization of Ennomini and Ourapterygini by Beljaev (2008), as results are also consistent with earlier hypotheses (e.g. Sihvonen et al. 2011). All austral South American taxa, i.e. *Atopodes* Warren, 1906, monotypic *Gonogala* Butler, 1882, *Microclysia* Butler, 1882, *Syncirsodes* Butler, 1882, and "*Tetracis*" *edmondsii* Butler, 1882 (not congeneric with true *Tetracis* Guenée, [1858]) are found in a single, well supported clade. In contrast, Nearctic species are widely scattered between 14 independent lineages within Ennomini (see discussion of biogeography below). In our analysis, Ennomini comprise the highest number of Neotropical genera (more than 100, including undescribed taxa) in a single tribe. Most genera were already assigned to this tribe by Pitkin (2002) (as Ourapterygini), but many also to the related informal *Cratoptera*-group, to the related Nephodiini, and a few to Caberini and Nacophorini, while more than 60 were left unassigned by Pitkin (2002). Beljaev (2008) synonymized Nephodiini and the *Cratoptera* group (misspelled as *Catoptera* group) with the Ennomini, and assigned many previously unassigned taxa to Ennomini. Our data clearly confirm the synonymy of Nephodiini with Ennomini, but the broad-scale assignment of taxa by Beljaev (2008) requires additions and adjustment in several cases (Table 3). Three species are transferred from unassigned to Ennomini, but genus combinations are incertae sedis: "*Acrotomia*" *mucia* Druce, 1892, "*Bassania*" *crocallinaria* Oberthür, 1883 and "*Cyphoedma*" *transvolutata* Walker, 1860 (Table 3). In addition to the list provided by Beljaev (2008), the genera *Acrosemia* Herrich-Schäffer, [1855], *Eutomopepla* Warren, 1894, *Microgonia* Herrich-Schäffer, [1855], *Polla* Herrich-Schäffer, [1855], and *Tarma* Rindge, 1983, are transferred to Ennomini (Table 3). *Brachyctenistis* Warren, 1904 is transferred from Nacophorini to Ennomini (Table 3).

Ennomini comprise several non-monophyletic genera. For these cases, we suggest that the respective generic names should be listed – ad interim – with quotation marks (Pitkin 2002; Scoble 1999) and integrative revisions of the mentioned taxa are required to provide new nomenclatorial combinations. "*Mychonia*" *galanata* Dognin, 1895 is not congeneric with type species-related members of *Mychonia* Herrich-Schäffer, [1855] (Table 3) and is also morphologically rather distinct (illustrated in Electronic Supplement File 5). The same applies for "*Isochromodes*" *analiplaga* Warren, 1907 and "*Isochromodes*" *sabularia* Dognin, 1900 which are not congeneric with true *Isochromodes* Warren, 1894 – already suspected by Pitkin (2002) (Table 4). *Nephodia nubilaria* Hübner, 1823 is the type species of the genus, whereas many other taxa currently assigned to *Nephodia* Hübner, 1823 most likely need to be transferred to other genera in future studies. One option is the re-erection of *Nipteria* Guenée, [1858] that would include the sampled species *panacea* Thierry-Mieg, 1892 (Fig. 7G) and presumably many other species currently assigned to *Nephodia*. *Sabulodes* Guenée, [1858] is represented by the type species of the genus, *S. caberata* Guenée, [1858] which does not cluster together with "*Sabulodes*" *thermidora* Thierry-Mieg, 1894. *Enypia* Hulst, 1896 is nested within *Sabulodes* and is therefore synonymized (Table 3). *Nematocampa* Guenée, [1858] is represented by its North American type species *N. resistaria* Herrich-Schäffer, [1856] (*filamentaria* Guenée, [1858] is a junior synonym). Neotropical *N. angulifera* Oberthür, 1883 clusters with *N. resistaria*. "*Nematocampa*" *confusa* Warren, 1904 was already excluded from this genus by Pitkin (2002) and "*Nematocampa*" *falsa* Warren, 1906 was suspected to be misplaced by Pitkin (2002) (Table 3). True *Melinodes* Herrich-Schäffer, [1855] are closely related to *Nematocampa* and these genera share the tentacle-like structures of the larvae (Brehm 2003), a potential synapomorphy of the lineage. Two species analysed in this study, "*Melinodes*" *fulvitincta* Warren, 1905 and "*Melinodes*" *ignea* Warren, 1907, were previously excluded from the genus by Pitkin (2002), and our results support this view. *Perusia* Herrich-Schäffer, [1855] is represented in our tree by three species, all of which represent independent lineages. "*Perusia*" *zoma* (Dognin, 1896) and "*Perusia*" *viridis* Warren, 1907 appear to be misplaced (Fig. 7H, Table 3). The latter species shares green pigmentation with the closely related genus *Phyle* Herrich-Schäffer, [1855], a potential synapomorphy of this lineage. "*Eusarca*" *bogotata* Snellen, 1874 does not cluster together with *Eusarca nemora* Druce, 1892, a species that closely resembles the type species of the genus (Electronic Supplement File 5, Table 3). A similar case are "*Anisoperas*" near *tessellata* Walker, [1863] and *Anisoperas proxima* Dognin, 1914 (Electronic Supplement File 5, Table 3).

4.6.9. Unnamed clade. A well supported clade is formed by *Declana* Walker, 1858, from New Zealand, probably representing an undescribed tribe.

4.6.10. Campaeini + Alsophilini + Wilemaniini + Prosopolophini clade. Each tribe is represented by only one or two species in our analysis. The Central American species *Himeromima aulis* Druce, 1892 (Fig. 7I) could not be assigned to a tribe by Pitkin (2002), and our results suggest that it either forms an own lineage or is part of the Prosopolophini. We here assign monotypic *Himeromima* Warren, 1904 to Prosopolophini (Table 3). The clade certainly requires a more comprehensive taxon sampling in future studies.

Table 3. Taxonomic changes in Ennominae at the level of tribes, genera and species, in alphabetical order. *Old World taxa.

Synonymized tribes	**Valid tribes**
Azelinini Forbes, 1948 **syn.n.**	Odontoperini Tutt, 1896
New tribes	**Included taxa**
Euangeronini **new tribe**	*Euangerona* Butler, 1882, "*Chloroclydon" rinodaria* Felder & Rogenhofer, 1875, *Dectochilus* Butler, 1882, *Odontothera* Butler, 1882, *Malleco* Rindge, 1971, "*Opisogonia" diffissata* Felder & Rogenhofer, 1875
Oenoptilini, **new tribe**	*Neobapta* Warren, 1905, *Oenoptila* Warren, 1895
Pyriniini **new tribe**	*Pyrinia* Hübner, 1818, *Acrotomia* Herrich-Schäffer, *Acrotomodes* Warren, 1895, *Falculopsis* Dognin, 1913, *Trotogonia* Warren, 1905
Synonymized genera	**Valid genus**
Nepitia Walker, 1866 **syn.n.**	*Pero* Herrich-Schäffer, 1855
Enypia Hulst, 1896 **syn.n.**	*Sabulodes* Guenée, [1858]
Species proposed to be excluded from genera = *incertae sedis*	**Tribe assignment, country, originally described in genus**
"*Anisoperas" tessellata* (Walker, [1863]) (analysed)	Ennomini, Brazil, *Hyperetis?*
"*Anisoperas" albimorsa* Warren, 1905	Ennomini, Peru, *Anisoperas*
"*Eusarca" bogotata* (Snellen, 1874) (analysed)	Ennomini, Colombia, *Epione*
"*Hypomecis" ectropodes* (Prout, 1913) (analysed)*	unassigned, South Africa, *Boarmia*
"*Isochromodes" analiplaga* Warren, 1907 (analysed)	Ennomini, Peru, *Paracomistis*
"*Isochromodes" sabularia* Dognin, 1900 (analysed)	Ennomini, Ecuador, *Organopoda?*
"*Mychonia" galanata* Dognin, 1895 (analysed)	Ennomini, Ecuador, *Mychonia*
"*Nematocampa" falsa* Warren, 1906 (analysed)	Ennomini, French Guyana, *Nematocampa*
"*Sabulodes" thermidora* (Thierry-Mieg, 1894) (analysed)	Ennomini, Bolivia, *Epione?*
"*Perusia" zoma* (Dognin, 1896) (analysed)	Ennomini, Ecuador, *Acidalia*
"*Perusia" viridis* Warren, 1907 (analysed)	Ennomini, Peru, *Perusia*
Tribe transfer	**Taxon**
Boarmiini to Macariini	*Dasyfidonia* Packard, 1876
Boarmiini to unassigned	*Bryoptera* Guenée, [1858]
Caberini to Ennomini	*Acrosemia* Herrich-Schäffer, [1855]
Caberini to Ennomini	*Microgonia* Herrich-Schäffer, [1855]
Caberini to unassigned	*Erastria* Hübner, [1813]
Caberini to unassigned	*Sericosema* Warren, 1895
Cassymini to unassigned	*Ballantiophora* Butler, 1881
Cassymini to unassigned	*Berberodes* Guenée, [1858]
Cassymini to unassigned	*Cirrhosoma* Warren, 1905
Cassymini to unassigned	*Hemiphricta* Warren, 1906
Cassymini to unassigned	*Hypometalla* Warren, 1904
Cassymini to unassigned	*Phaludia* Schaus, 1901
Ennomini to Boarmiini	*Mnesipenthe* Warren, 1895
Ennomini to Gnophini	*Neorumia* Bartlett-Calvert, 1893
Ennomini to Odontoperini	*Henicovalva* Krüger, 2017
Ennomini to Palyadini	*Pityeja* Walker, 1861
Ennomini to unassigned	*Idialcis* Warren, 1906
Hypochrosini to Epionini	*Metanema* Guenée, [1858]
Lithinini to Odontoperini	*Talca* Rindge, 1971
Nacophorini to Ennomini	*Tarma* Rindge, 1983
Nacophorini to Ennomini	*Brachyctenistis* Warren, 1904
Nacophorini to Odontoperini	*Dentinalia* Heimlich, 1960
Nacophorini to Odontoperini	*Macrolyrcea* Butler, 1882
Nacophorini to Odontoperini	*Mallomus* Blanchard, 1852
Nacophorini to Odontoperini	*Praeantarctia* Heimlich, 1956
unassigned to Cassymini	*Orbamia* Herbulot, 1966*
unassigned to Cassymini	*Pycnostega* Warren, 1905*
unassigned to Boarmiini	"*Synnomos" apicistrigata* Warren, 1895
unassigned to Ennomini	"*Acrotomia" mucia* Druce, 1892
unassigned to Ennomini	"*Bassania" crocallinaria* Oberthür, 1883
unassigned to Ennomini	"*Cyphoedma" transvolutata* Walker, 1860

Table 3 continued.

unassigned to Ennomini	*Eutomopepla* Warren, 1894
unassigned to Ennomini	"*Neorumia*" *gracilis* Bartlett-Calvert, 1893
unassigned to Ennomini	*Polla* Herrich-Schäffer, [1855]
unassigned to Nacophorini	*Eustenophasma* Warren, 1897
unassigned to Nacophorini	*Leucochesias* Mabille, 1899
unassigned to Odontoperini	*Nemeris* Rindge, 1981
unassigned to Prosopolophini	*Himeromima* Warren, 1904
New generic combinations	**Originally described in genus, transferred from genus, decision based on**
Bryoptera vaga (Dognin, 1895) **comb.n.**	*Tephrosia*, "*Ectropis*", molecular data and external morphology

4.6.11. Diptychini. Murillo-Ramos et al. (2019) synonymized Lithinini with Diptychini. A well supported clade comprises former Lithinini including the Holarctic name-bearing genus *Petrophora* Hübner, [1811] with samples both from North America and Europe. Apart from the Palaearctic genera, the former core Lithinini also comprises Neotropical "*Loxaspilates*" (Fig. 7J), (not congeneric with the Asian Gnophini genus *Loxaspilates* Warren, 1893) and *Neazata* Warren, 1906. *Neazata* was transferred from Caberini to Diptychini by Murillo-Ramos et al. (2019). Three Chilean genera were previously assigned to Lithinini: *Tacparia* Walker, 1860, *Martindoelloia* Orfila & Schajovski, 1963, and *Tanagridia* Butler, 1882 (Pitkin 2002). Another clade, exclusively comprising austral South American taxa comprises *Euclidiodes* Warren, 1895, *Franciscoia* Orfila & Schajovski, 1963, *Psilaspilates* Butler, 1893, and *Rhinoligia* Warren, 1895. Further Diptychini include two large clades. Genera belonging to a clade of Australian taxa previously assigned to Nacophorini were transferred to Diptychini by Murillo-Ramos et al. (2019). Another clade comprises African taxa previously assigned to Lithinini, to Nacophorini, to Diptychini or that were unassigned.

4.6.12. Oenoptilini Brehm, Murillo-Ramos & Sihvonen, new tribe. — **Type genus.** *Oenoptila* Warren, 1895 (Fig. 7K). — **Material examined and phylogeny.** Our analysis comprises *O. mixtata* Guenée, [1858], the type species of *Oenoptila*. *Neobapta* Warren, 1904 is also included in the tribe. Branch support values from the IQ-TREE analyses clearly confirm the monophyly of Oenoptilini (SH-like = 99.6, UFBoot2 = 100). However, the deeper phylogenic relationships of the tribe are unresolved. — **Molecular evidence.** The tribe is characterized by DNA sequence data from the following nine gene regions (exemplar *Oenoptila mixtata*, voucher Br-Geo-0006 from Brazil, illustrated in Electronic Supplement File 5): ArgK (MK738208), Ca-ATPase (MK738605), CAD (MK738934), COI (MK739100), EF1a (MK740300), MDH (MK740945), Nex9 (MK741374), RPS5 (MK741714), Wingless (MK742175). — **Morphology.** *Oenoptila* and *Neobapta* are structurally dissimilar: *Oenoptila* are characterised by a pair of sclerotised, finger-like processes of the juxta, which are tipped with a pouch. *Neobapta* has multiple pairs of coremata and leaf-shaped process of the anallus. These genera share the densely setose valva (illustrated in Pitkin 2002). External features of analysed species are illustrated in Fig. 7K and Electronic Supplement File 5. Further detailed morphological analysis is required to identify potential diagnostic features. — **Remarks and taxonomic changes.** *Neobapta* and *Oenoptila* were previously assigned to Caberini by Pitkin (2002). However, true Caberini (comprising Old and New World *Cabera* Treitschke, 1825) form a separate clade phylogenetically distant from Oenoptilini, see 4.6.19 below.

4.6.13. Baptini + Theriini clade. Baptini (*Lomographa* Hübner, [1825]) are not closely related to Caberini. Baptini and Theriini form a well supported clade and *Lomographa* is represented with species from Europe (*L. bimaculata* Fabricius, 1775) and Ecuador (unidentified species).

4.6.14. Unnamed clade. This well supported lineage comprises New World *Erastria decrepitaria* Hübner, [1823], Madagascan and Afrotropical *E. madecassaria* Boisduval, 1833 – and nested among these species, Nearctic *Metarranthis obfirmaria* Hübner, [1823]. We exclude *Erastria* from Caberini (Table 3) and suggest more study on *Erastria* and its relationship (and possible synonymy) with *Metarranthis*, but current taxon sampling is too limited for formal changes.

4.6.15. Plutodini + Palyadini clade. Old World *Plutodes* Guenée, [1858] (Plutodini) is sister to Neotropical Palyadini that were revised by Scoble (1994) and Pitkin (2002). However, in the RAxML tree, *Plutodes* is sister to *Eumelea*, and both are sister to Pyrinini (Murillo-Ramos et al. 2019). Our analysis of Palyadini comprises *Argyrotome* Warren, 1894, *Ophthalmoblysis* Scoble, 1995 (Fig. 7L), *Opisthoxia* Hübner, [1825], *Palyas* Guenée, [1858], *Pityeja* Walker, 1861 and *Phrygionis* Hübner, [1825]. Without obvious reason, Beljaev (2008) transferred *Pityeja* to Ennomini; we hereby reverse this transfer (Table 3).

4.6.16. Apeirini + Epionini + Anagonini + Hypochrosini clade. Because the four tribes are represented only by between one and three species, they are treated here together. The clade comprises representatives of four mostly Old World tribes: Apeirini (*Apeira* Gistl, 1848),

Epionini (*Epione* Duponchel, 1829), Anagonini (*Probole* Herrich-Schäffer, [1855] and *Plagodis* Hübner, [1823], and Hypochrosini (*Hypochrosis* Guenée, [1858]). Three Nearctic taxa are present in this lineage, and we propose to change the tribe assignment of two taxa: *Metanema* Guenée, [1858] is transferred from Hypochrosini to Epionini. *Sericosema* Warren, 1895 (Fig. 7M) is excluded from Caberini, but remains unassociated with tribe (Table 3).

4.6.17. Drepanogynini. This tribe was described by Murillo-Ramos et al. (2019). Sister to the aforementioned clade, this well supported tribe comprises four African genera that previously were assigned to Nacophorini.

4.6.18. Pyriniini Brehm, Murillo-Ramos & Sihvonen, new tribe. — **Type genus.** *Pyrinia* Hübner, 1818 (Fig. 7N). — **Material examined and phylogeny.** In addition to *Pyrinia*, this clade comprises *Acrotomia* Herrich-Schäffer, [1855], *Acrotomodes* Warren, 1895, and *Trotogonia* Warren, 1905. Branch support values from the IQ-TREE analyses clearly confirm the monophyly of Pyriniini (SH-like = 100, UFBoot2 = 100). The tribe forms a well suppported clade with Caberini, and tribes around Cassymini (4.6.19.–4.6.20.) but it is uncertain which is sister to Pyriniini. — **Molecular evidence.** The tribe is characterized by DNA sequence data from the following five gene regions (exemplar *Pyrinia abditaria*, Warren, 1905, voucher gb-ID-17449 from Ecuador, illustrated in Electronic Supplement File 5): CAD (JF785178), COI (JF784698), EF1a (JF785322), MDH (JF784839), RPS5 (JF784951). — **Morphology.** Pitkin (2002) already recognized the group and suggested the pair of setose processes adjoining the juxta postero-laterally in the male genitalia as a synapomorphy (*Acrotomodes*, *Falculopsis* Dognin, 1913, and *Pyrinia*). They also share the divided valva (not present in all species), and extended chaetosemata on dorsal side of head. Externally the species are very diverse, see Fig. 7N and Electronic Supplement File 5. — **Remarks and taxonomic changes.** Because of Pitkin's (2002) study, we also include *Falculopsis* in Pyriniini (Table 3).

4.6.19. Caberini. Our data (and those of previous molecular analyses) do not support a close relationship of Baptini and Caberini, e.g. as suggested by Pitkin (2002). Many New World taxa assigned to Caberini by Pitkin (2002) are not part of this clade (e.g. *Paragonia* Hübner, [1823], *Neazata*, *Oenoptila*), but belong to Ennomini, Diptychini and Oenoptilini, respectively (see above). On the other hand, the Neotropical genera *Aplogompha* Warren, 1897 (Fig. 7O), *Lobopola* Warren, 1900, *Sphacelodes* Guenée, [1858], and *Thysanopyga* Herrich-Schäffer, 1855, are Caberini indeed, as well as the Nearctic genera *Apodrepanulatrix* Rindge, 1949, *Chloraspilates* Packard, 1876, *Eudrepanulatrix* Rindge, 1949, and *Ixala* Hulst, 1896. *Cabera* Treitschke, 1825 in its current limits is polyphyletic, obviously requiring revision.

4.6.20. Cassymini + Abraxini + Eutoeini + Macariini clade. This well supported clade (SH-like = 99.9, UFBoot2 = 100) comprises Cassymini, Abraxini, Eutoeini and Macariini. The majority of the recovered phylogenetic relationships between the clades is, however, poorly supported. The clade is strongly supported as sister group to Boarmiini, and all four tribes have previously been proposed to form a monophylum based on shared morphological traits, *viz*. reduction of the pupal cremaster to a pair of strong spines and the presence of a forewing fovea (Holloway 1994; Holloway et al. 2001). While most of the investigated taxa can safely be assigned to one of the four tribes, eight genera can currently not be assigned to tribe, namely African *Dorsifulcrum* Herbulot, 1979, Palaearctic *Odontognophos* Wehrli, 1951, and New World *Ballantiophora* Butler, 1881, *Berberodes* Guenée, [1858], *Cirrhosoma* Warren, 1905, *Hemiphricta* Warren, 1906, *Hypometalla* Warren, 1904 (Fig. 7P, Table 3), and *Phaludia* Schaus, 1901. Up to four clades might represent tribes of their own, but further investigation and broader taxon sampling is required.

Cassymini s.l. has modest support (SH-like = 65.7, UFBoot2 = 66), whereas Cassymini s.str. is well supported (SH-like = 100, UFBoot2 = 97). Cassymini s.str. comprises several Old World genera (including the species-rich genus *Zamarada* Moore, [1887]) as well as Nearctic *Protitame* McDunnough, 1939. Ferguson (2008) also included *Nematocampa*, which is hereby transferred to Ennomini (see above), and *Taeniogramma* Dognin, 1913 (not sampled in this study). A clade that comprises Neotropical *Leuciris* Warren, 1894 (Fig. 7Q), as well as African *Orbamia* Herbulot, 1966, and *Pycnostega* Warren, 1905 is sister to Cassymini s.str.. We transfer *Pycnostega* and *Orbamia* from unassigned to Cassymini (Table 3). Abraxini is well supported (SH-like = 99.7, UFBoot2 = 94). Abraxini has no representatives in the Neotropical region (Pitkin 2002). Ferguson (2008) considered *Ligdia wagneri* Ferguson & Adams, 2008 to be the sole representative of Abraxini in North America while all other species of *Ligdia* Guenée, [1858] occur in the Palaearctic region (Scoble 1999). Eutoeini is also well supported (SH-like = 98.2, UFBoot2 = 99) and appears to be absent from the New World.

Macariini is perfectly supported (SH-like = 100, UFBoot2 = 100) and is divided between two diverse lineages based around *Macaria* Curtis, 1826 (Old World and New World) (Fig. 7R) and *Chiasmia* Hübner, [1823] (Old World), respectively. Both genera were resolved as monophyletic, although our taxon sampling was limited. Macariini assignment is confirmed for *Digrammia* Gumppenberg, 1887, *Eumacaria* Packard, 1873, *Isturgia* Hübner, [1823], *Heliomata* Grote & Robinson, 1866, and *Narraga* Walker, 1861. *Dasyfidonia* Packard, 1876 is transferred from Boarmiini to Macariini (Table 3). McGuffin (1977) considered *Dasyfidonia* as being related to *Hypagyrtis* Hübner, 1818, based on similarities in genitalic morphology, wing venation and the presence of a forewing fovea; Ferguson (2008) did not mention *Dasyfidonia* in relation to the North American Macari-

ini. *Dasyfidonia* differs considerably from most Nearctic Boarmiini in genitalic structure, but is surprisingly similar to *Isturgia*, *Eumacaria*, *Trigrammia* Herrich-Schäffer, [1855] and *Mellilla* Grote, 1873, sharing strongly and smoothly emarginate male valve and the presence of a prominent, scoop-like gnathos. Wing shape and pattern elements of *Dasyfidonia* are also more similar to Macarini, sharing the prominent three transverse forewing lines and absence of discal spots.

4.6.21. Boarmiini. This extremely large clade is probably the best-sampled tribe of Ennominae and will be treated in a separate paper by L. Murillo-Ramos et al. (in prep.). Jiang et al. (2017) concentrated their sampling on the Oriental and Palaearctic region, and our study complements this with material from the New World, Africa and other regions. The clade does not only include "typical" well camouflaged boarmiines but also conspicuously coloured genera such as *Perigramma* Guenée, [1858] (Fig. 7S). We transfer *Mnesipenthe* Warren, 1895 from Ennomini (Beljaev 2008) to Boarmiini (Table 3). "*Synnomos*" near *apicistrigata* Warren, 1895 is transferred from unassigned to Boarmiini (Fig. 7T, Table 3).

4.7. Biogeographic patterns

We make some remarks with regard to New World taxa here, but a global biogeographic analysis of the family Geometridae is planned (H. Ghanavi et al. in prep.). Figures 1, 2, 4, 6 provide an overview of some major biogeographic patterns with regard to the New World, shown in detail in Electronic Supplement File 2 (all New World taxa are marked with colour). New World taxa are not randomly distributed in the tree, but usually form more or less large clusters, indicating colonizing events followed by local diversification. While the taxon sampling is now very good in the New World, much more sampling is required in other regions. Despite these principal limitations, the results allow us some preliminary conclusions. While Nearctic and Neotropic taxa are often intermixed, the austral South American taxa tend to be more isolated. This pattern is consistent with long recognized biogeographic patterns showing a separation of South America into a tropical northern/central region on the one hand, and a southern temperate region on the other (Morrone 2015). The southern region still has biogeographic connections to other southern temperate regions due to their peleogeographic connection via Antarctica (Sanmartín & Ronquist 2004). Morrone (2006) placed the entomofauna of southern South America in the "Austral Kingdom", together with Australia, South Africa and New Zealand, and separate from the Neotropics. On the other hand, Holt et al. (2013), analysing distribution and phylogenetic relationships of vertebrates, placed all of South America in the Neotropical faunal realm, though separated into rather distinct northern and southern regions. Currently, our data do not show any strong connections that indicates an "Austral Kingdom" of geometrid moths, but a clear isolation of the austral South American fauna is evident (Andean Region). Further taxon sampling in southern Africa, Australia and New Zealand is required for a more complete view.

Figures 1 – 2 and 5 – 6 demonstrate that many lineages are dominated by New World taxa or are even restricted to this region. Many exclusively New World lineages are described as new tribes in this paper, highlighting the previous systematic bias, pointed out by e.g. Õunap et al. (2016). On the other hand, many lineages are restricted to other parts of the World. However, even our sampling in the New World is still incomplete and some species-rich genera were not sampled although they form diverse groups in the Neotropical region also (for example, the genera *Scopula* and *Eupithecia*).

In Sterrhinae, Neotropical species are present in most major clades. *Idaea* Treitschke, 1825 is nested deeply within a Neotropical clade, suggesting that the ancestors of *Idaea* were Neotropical. *Dithecodes* Warren, 1900 is distributed in Asia and in the Neotropics – a rather exceptional biogeographic pattern that calls for more study. In Larentiinae-Trichopterygini, a clear nucleus of southern South American taxa is visible (Fig. 1) whereas only two samples are from the tropical parts of the continent (*Rhopalodes concinna* Dognin, 1911 and an unidentified genus + species). An Old World clade comprises *Trichopteryx* Hübner, [1825] as well as the Nearctic genus *Cladara* Hulst, 1896. In the Asthenini, *Eois* represents the single (and extremely large) radiation of the tribe in the Neotropics, and only two other Asthenini genera are known to have a Holarctic distribution. Psaliodini comprise both species from both the Neotropical region and austral South America. The clade with the highest number of New World taxa is formed of an unnamed lineage in the Larentiini complex (4.2.20.2. – 4.2.20.10.). This clade is currently mostly Neotropical with some nested austral South American and Nearctic taxa. Remarkably, *Stamnodes*, the type genus of Stamnodini is represented with a Nearctic and a Palaearctic species and nested deep within the clade. A Neotropical origin can also be assumed for *Spargania*: It is very diverse in the Neotropical region, less diverse in the Nearctic region, and only one species occurs also in the Palaearctic region.

In Geometrinae, New World representatives are restricted to only four distinct lineages in our dataset. This confirms previous findings (Pitkin 1996; Pohl et al. 2016). A large number of tribes are obviously restricted to the Old World. By far, the largest radiation is Nemoriini with Nearctic species nested within a large Neotropical clade. Due to rather good taxon sampling of Geometrinae (Ban et al. 2018), it can be concluded that these moths are likely to have an origin in the Old World, and that the New World was successfully colonized only a few times.

Ennominae is dominated by two large tribes, the Ennomini and the Boarmiini. These tribes show very different biogeographic patterns. Ennomini comprise mostly Neotropical taxa with many nested Nearctic taxa. Currently, five Old World Ennomini genera are all part of

a single clade that also comprises Nearctic taxa. Old World lineages of Ennomini are likely to increase with better taxon sampling, but currently available data suggests a Neotropical origin of Ennomini. On the contrary, Boarmiini show a completely different pattern: In this tribe, the New World was probably colonized by many independent lineages from the Old World. Since taxon sampling in the New World is good, it is unlikely that the current view will be challenged with denser taxon sampling. In Boarmiini, colonization has probably primarily occurred from the Palaearctic to the Nearctic region. New World taxa are mostly concentrated in only two larger radiations, one around *Physocleora* Warren, 1897, *Glena* Hulst, 1896 and *Iridopsis* Warren, 1894, and one around *Prionomelia* Warren, 1895, *Melanolophia* Hulst, 1896 and *Carphoides* McDunnough, 1920. The latter three genera, in addition to six other genera, formed the former Melanolophiini (McGuffin 1987). In addition, a large number of distinct lineages with one or more representatives occurring in the New World are widely scattered in the tree: *Aethalura* McDunnough, 1920, *Epimecis* Hübner, [1825], *Hesperumia* Packard, 1873, *Hypagyrtis* Hübner, 1818, *Orthofidonia* Packard, 1876, *Paleacrita* Riley, 1876, *Protoboarmia* McDunnough, 1920 and "*Synnomos*" near *apicistrigata* Warren, 1895. Most of these genera are phylogenetically isolated in the New World, but have close relatives in Eurasia. For example, *Orthofidonia* is closely related to the Eurasian genera *Arichanna* Moore, 1868, and *Bupalus* Leach, [1815], in addition to the genera that are primarily Eurasian with one or few Nearctic representatives: *Biston* Leach, [1815], *Hypomecis* Hübner, 1821, *Lycia* Hübner, [1825], and *Phigalia* Duponchel, 1829. These Nearctic boarmiine genera form a considerable portion of the geometrid fauna of the deciduous forest regions of eastern North America, and their evolutionary links to Eurasia hint at similarities to that of Tertiary relict plant distributions (Milne & Abbott 2002). Genera, or even species with clearly Holarctic distributions are concentrated in the boreal forest region of the northern Nearctic, where genera such as *Dysstroma*, *Thera*, *Lampropteryx*, *Epirrita*, *Operophthera*, *Epirrhoe*, *Scopula*, and *Xanthorhoe* comprise a significant portion of the total geometrid diversity. In contrast, the arid and semi-arid regions of the southwestern Nearctic is dominated by lineages with Neotropic origins, particularly the Boarmiini, Nacophorini, Psaliodini, and Pterocyphini.

5. Conclusions

Our study comprises hundreds of New World Geometridae taxa that have not been included in a phylogenetic study before. It significantly pushes the New World geometrid fauna from one of the phylogenetically least studied to one of the best studied lepidopteran taxa, along with a series of related papers (see Introduction). It was our goal not "only" to provide a phylogenetic hypothesis, but also to translate many of the results into taxonomy. We are well aware that this was a balancing act: On the one hand, we did not want to produce another phylogenetic study suggesting required changes but not performing them. On the other hand, it was beyond the scope of our study to deeply examine the morphology of a broad range of taxa. One might argue that the description of nearly a dozen new tribes requires a detailed morphological study of each taxon. We agree that morphological studies are indeed needed and data should be analysed in a future integrative approach. However, we think that our data offer a sufficient basis for many taxonomic changes, and we only performed them in "clear" cases in terms of branch support and available generic names – and in agreement with ICZN regulations on the establishment of new family group names. Should some of our hypotheses be falsified in future studies, it is well possible that some names will be synonymized. We regard this as a normal process when more, both morphological and molecular data will become available, particularly for African and Australian taxa. However, until we will know better in the future, providing names for otherwise unnamed clades in Geometridae significantly eases communication in the community. Our paper, including illustrated catalogues of nearly all sampled New World taxa, assigns many taxa for the first time to tribe. Moreover, it is a basis for future taxonomic work, and we believe it will ease the description and assignment of a large number of taxa, including many new generic names and new generic combinations. We hope that our paper stimulates further research on New World geometrids, particularly in taxonomy and ecology.

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Authors' contributions

The idea for a series of contributions to Geometridae phylogeny was by G.B., P.S. and N.W. G.B. has coordinated the taxon sampling for New World taxa. G.B. and all other authors have written the manuscript. Material was sampled by G.B., L.M.-R., A.H., B.C.S., E.Õ., A.M., D.B., F.B., R.M., and A.L. L.M.-R. has performed most of the laboratory work and the data analysis. G.B. has prepared figures, tables and the supplement files.

Electronic Supplement Files

at http://www.senckenberg.de/arthropod-systematics

File 1: brehm&al-geometridaenewworld-asp2019-electronicsupplement-1.pdf — IQ tree including all taxonomic changes, tribes colour-coded.

File 2: brehm&al-geometridaenewworld-asp2019-electronicsupplement-2.pdf — IQ tree including all taxonomic changes, regions colour-coded.

File 3: brehm&al-geometridaenewworld-asp2019-electronicsupplement-3.pdf — Illustrated pdf catalogue of analysed New World small subfamilies (Sterrhinae, Geometrinae, Archiearinae, Desmobathrinae).

File 4: brehm&al-geometridaenewworld-asp2019-electronicsupplement-4.pdf — Illustrated pdf catalogue of analysed New World Larentiinae.

File 5: brehm&al-geometridaenewworld-asp2019-electronicsupplement-5.pdf — Illustrated pdf catalogue of analysed New World Ennominae.